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THE NATURAL HISTORY OF NATIVE FISHES IN THE DEATH VALLEY SYSTEM

By David L. Soltz and Robert J. Naiman

NATURAL HISTORY MUSEUM
OF LOS ANGELES COUNTY
In Conjunction With
THE DEATH VALLEY
NATURAL HISTORY ASSOCIATION

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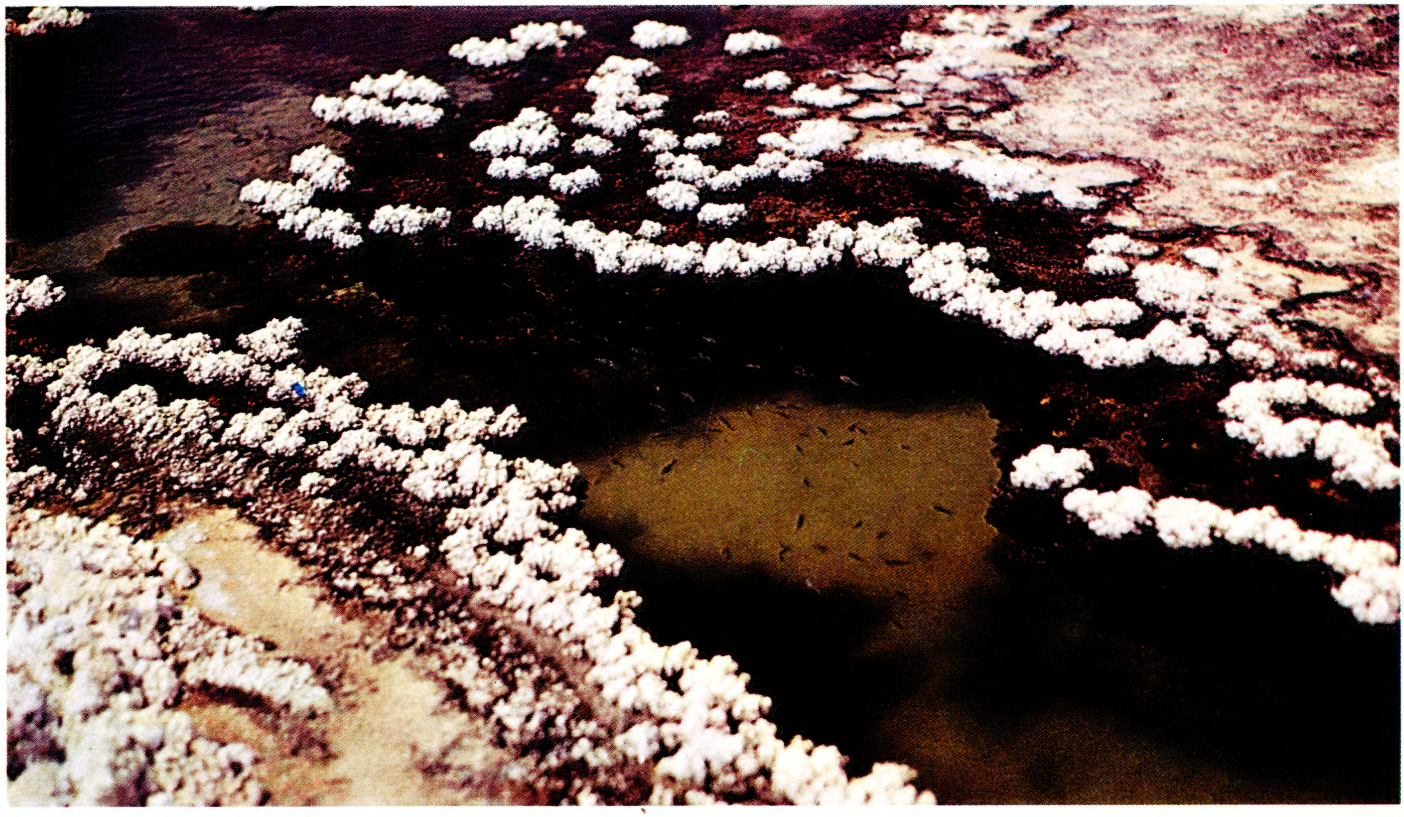
COVER: Big Spring, Ash Meadows, Nevada. Alan Heller.

Death Valley Fishes



FRONTISPIECE: Cottonball Marsh, Death Valley National Monument. Robert Naiman.

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By David L. Soltz and Robert J. Naiman

Illustrated by Carol Mortensen

NATURAL HISTORY MUSEUM
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To
CARL L. HUBBS

for his life-long dedication to preserving America's
desert fishes

TABLE OF CONTENTS

Acknowledgments ix

Introduction 1

Geological, Climatic, and Hydrological Setting 3

Pleistocene Hydrography 3

Recent Hydrography 5

History and Evolution of Fishes in the Death Valley System 7

History 7

Evolution 9

Present Distribution and Habitats 11

The Fishes 11

The Habitats 31

Natural History, Behavior, and Ecology 45

Life History and Behavior 45

Population Dynamics, Growth, and Production 49

Physiological Ecology 54

Conservation of Desert Fishes 65

Literature Cited 74

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Death Valley Fishes

INTRODUCTION

"No human being, however great, or powerful, was ever so free as a fish."
John Ruskin, *The Two Paths*. Lecture 5.

When most people think of deserts they do not associate fishes with their thoughts; fishes and deserts do not seem suited for each other. Yet, as one becomes more familiar with arid lands and discovers the widely spaced springs and small streams, they are surprised to find them often inhabited by tiny fish, remnants of the last Ice Age. These fishes have evolved over the last 2,000 to 20,000 years into many new species adapted to small, and sometimes harsh, aquatic habitats (Miller 1948). Although deserts are not known for diverse fish faunas, these fishes are important, possessing exceptional characteristics. For example, they present one of the clearest illustrations of the evolutionary process in North America, rivaling in diversity the finches of the Galápagos Islands which first caused Charles Darwin to crystalize his ideas on the evolutionary process.

Further, these fishes reflect the quality of life in deserts because water provides habitat not only for fish but also for bighorn sheep, bobcat, coyote, birds, amphibians, reptiles, and invertebrates. Literally hundreds of species of animals and plants, several of which are rare and endangered, depend upon aquatic habitats for survival. A continuous source of water is also responsible for a number of spectacular geological formations, of which the Devils Golf Course in the southern portion of Death Valley is probably the best known. Many Death Valley System fishes have adapted to harsh environmental conditions such as high salinity and temperatures ranging from near 0°C in winter to about 36°C in summer (Brown and Feldmeth 1971; Naiman, *et al* 1976). They can survive nearly every environmental extreme except one; they must have water. At present several populations live in water only a few centimeters deep. The fish will disappear when the water is gone. However, as long as the fish survive in these oases, habitat will be available for other species, and the complex but fragile desert ecosystem will remain healthy.

In the Death Valley System there were 10 species of fish, one of which has become extinct recently, and nine occur nowhere else on earth. There are five species of pupfish (genus *Cyprinodon*), two species of killifish (genus *Empetrichthys,* one species is extinct), two species of minnow (genera *Gila* and *Rhinichthys*), and one sucker (genus *Catostomus*). Nearly every population possesses distinctive characters and, in total, have revealed a great wealth of knowledge about the process of evolution, physiological and behavioral adaptations to harsh environments, and about desert ecosystems. Trying to answer such seemingly easy questions as, "Where did the fish come from?", has taken years of effort by many biologists, geologists, hydrologists, and anthropologists. The story is still not completely known, but what has been learned so far has vastly increased our basic knowledge and understanding of evolution, formation of deserts, long-term climate changes, and cultures of primitive man. Many aspects of the diverse Death Valley System are still being investigated, but such studies will never be totally "complete" in this dynamic desert region.

The purpose of this book is to draw together what is currently known about native fishes and aquatic habitats of the Death Valley System and present a general treatment of their natural history, evolution, and conservation. It begins with a description of the geological and hydrological setting, followed by the history and evolution of the fishes. Each species is illustrated and described along with a discussion of its specific habitat. Their natural history, behavior, and ecology are considered also. The final section discusses conservation of both fishes and aquatic ecosystems in the Death Valley System. The latter subject is of immediate and critical importance.

This book is about the fishes and their habitats, but it is crucial to realize aquatic ecosystems do not stop at the water's edge. Beyond this artificial line are many additional species of plants and animals depending upon this water for survival. Understanding the significance of springs, streams, and marshes to the total desert ecosystem, and their conservation, is the key to preserving the beauty and fascination of this vast region.

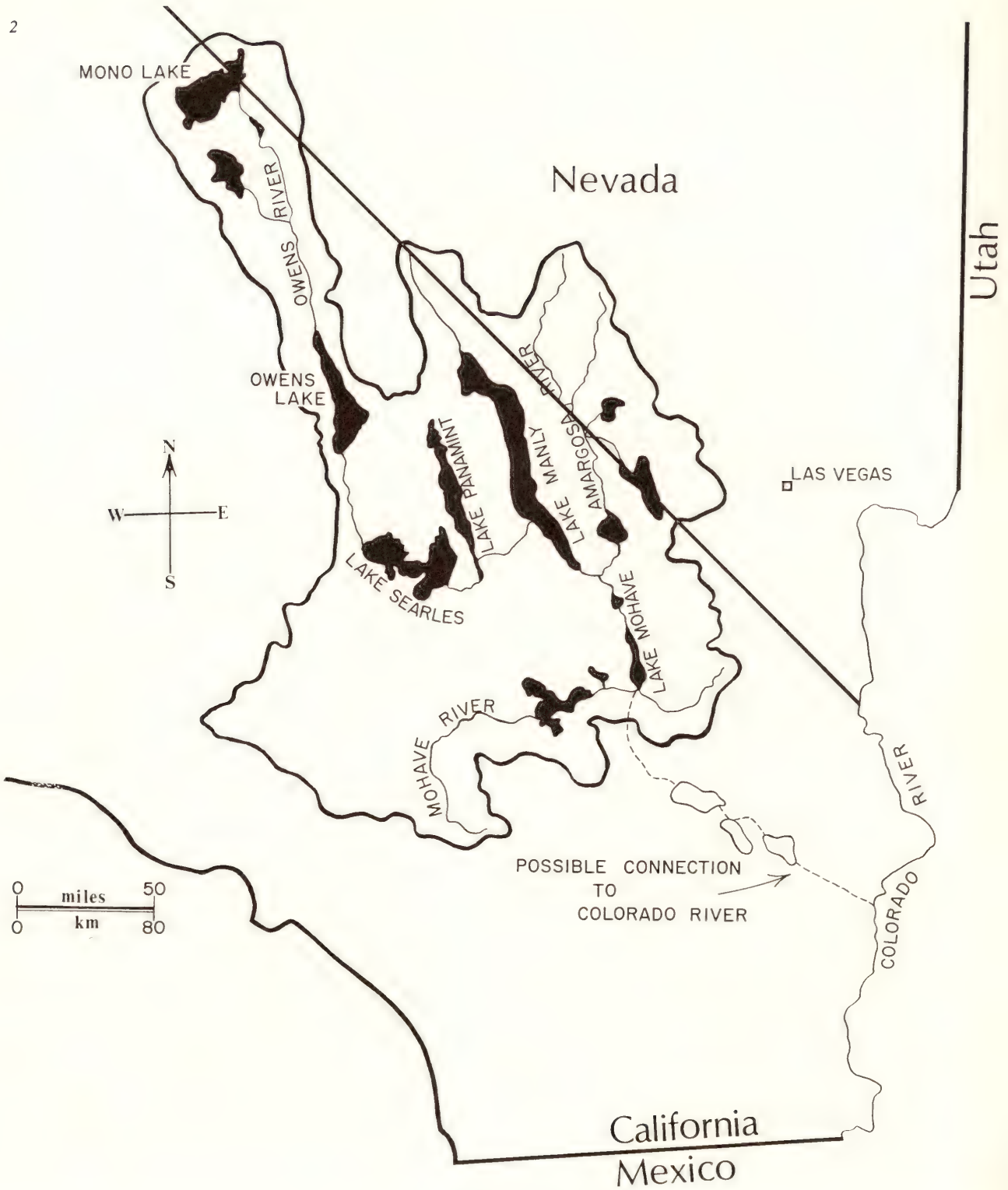

FIGURE 1. During the Pleistocene Epoch all basins within the Death Valley System contained large lakes interconnected by rivers. All lakes, however, may not have been contemporary. Some may have existed before or after others but the existence of related fish species in several of the basins argues well for extensive interbasin connections at one time. Many of the fishes in the Death Valley System are related to forms in the Colorado River Basin. Location of the connection between these two large systems is not well defined, but the probable route is shown on the map as a chain of unshaded lakes connected by the dotted line. This connection occurred long ago, probably in early or pre-Pleistocene time.

GEOLOGICAL, CLIMATIC AND HYDROLOGICAL SETTING

Till taught by pain,
men really know not what good water's worth
Byron, *Don Juan*. Canto ii, st. 84.

The Great Basin, of which the Death Valley System is a part, comprises most of Nevada and Utah with fringes in California, Oregon, Idaho and Wyoming. Despite the implication of its name, the province is not a single large basin surrounded by mountains, but is a combination of more than 90 valleys separated from each other by more than 160 mountain ranges (Blackwelder 1948; Miller 1948). Nearly all of these mountain ranges were formed by a geological process called block faulting, in which chunks of the earth's crust have been forced upward to form mountains, while other blocks have sunk to form valley floors. Almost all the basins have internal drainage (such as Death Valley), but a few are drained by tributaries of major river systems, particularly those of the Columbia and Colorado. Death Valley is a small but significant part of the Great Basin, showing many similarities with the rest of this vast desert region. Two of the most impressive similarities are the number of unique and endemic desert fishes occurring in the isolated desert basins, and the fact that much of the water providing habitat for these fishes originates outside the topographic valley and must flow long distances underground before its emergence in springs and streams.

Death Valley is regarded as the hottest and driest part of the United States (Hunt, *et al* 1966). Temperatures greater than 49°C are common from May to September; annual rainfall in the valley averages 4.22 centimeters (cm), with the annual precipitation in the entire hydrologic basin probably not exceeding 10–13 cm. In contrast, the evaporation rate in Death Valley is about 380 cm per year, and yet this region contains a highly varied and endemic fauna of aquatic organisms, including several fishes. Where does the water come from to support these animals? To answer this question it is necessary to explore the climatic, hydrologic, and geologic history of the Death Valley region.

Pleistocene Hydrography

During the latest stage of Pleistocene time (about 10,000 to 20,000 years ago) there existed in this desert region a group of interconnecting rivers named the Death Valley System because Death Valley formed the sump for the drainage (Miller 1948). The physiographic evidence for this river system is unmistakable, but the detailed history of the drainage has been complex and much of the story remains to be deciphered. The length of the Pleistocene Epoch is now believed to encompass nearly two million years during which there were at least four periods of much colder climate, each about 20–30 thousand years duration. During these colder intervals, called pluvials, glaciers formed in some of the higher mountains of the Great Basin. During the several coldest pluvials, when the temperature was probably 4–7°C below the long term average, the rate of evaporation was much lower and, hence, the region must have been decidedly less arid, even if there were no increase in precipitation. A surplus of winter snow formed ice fields at heads of mountain canyons, and long tongues of ice extended down toward the borders of the mountain ranges. At the same time, the formerly established balance between inflow (rainfall) and evaporation in the semiarid basins was tipped in favor of inflow. As a result, lakes developed in many topographically closed basins. Of these lakes, many of the large ones overflowed into adjacent basins and, thus, finally made contact with major rivers such as the Colorado and Columbia which flow into the Pacific Ocean (Hubbs and Miller 1948).

Death Valley was part of a much larger interconnected system which, during much of the Pleistocene Epoch, contained many large rivers and lakes. Aquatic organisms were able to move through streams between

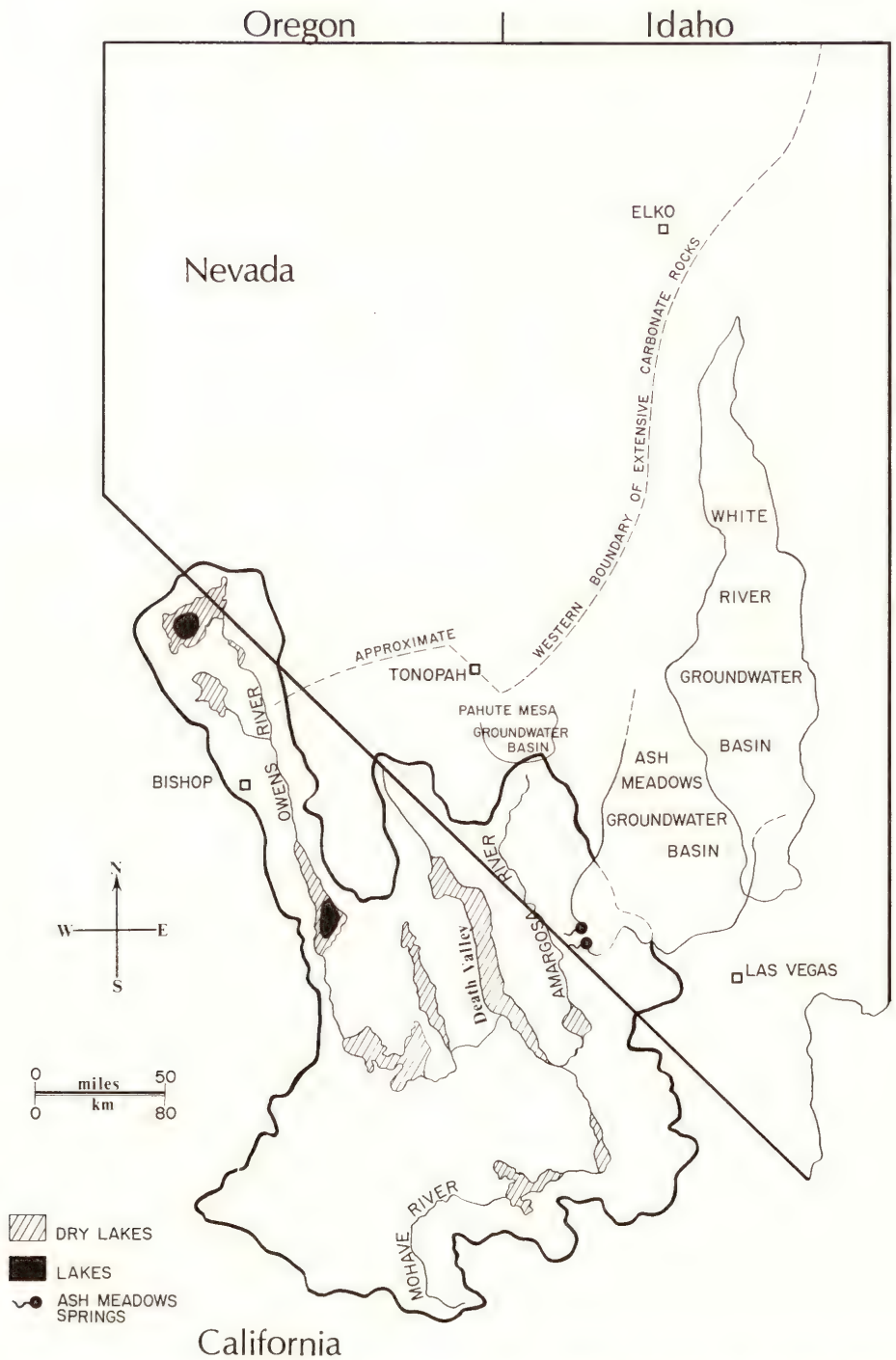

FIGURE 2. Today, hydrology of the Death Valley System is quite different from that of the Pleistocene Epoch. Owens Valley still receives water from precipitation in the Sierra Nevada and White Mountains, and the Mohave River receives runoff from the San Bernardino Mountains, but much of the water originates outside the drainage basin. Large amounts of water enter the Death Valley System from the northeast via underground movement through permeable carbonate rocks. The Pahute Mesa Groundwater Basin supplies the headwaters of the Amargosa River, and the Ash Meadows Groundwater Basin supplies the numerous springs in Ash Meadows and probably the eastern side of Death Valley. Limits of both these groundwater basins are not yet completely known but their areas are extensive. Water issuing from springs in Ash Meadows is 8,000 to 12,000 years old.

many of the basins. This is strongly supported by examining present day distribution of fishes throughout the Great Basin and especially in the Death Valley System. Some fishes presumably entered this region from the north via Mono Lake and Owens Lake, whereas others invaded from the south, most likely from the Colorado River System (Miller 1948; Pister 1974).

During the last glacial or pluvial period the Owens River, originating in the Sierra Nevada Mountains north of Bishop, California, overflowed its present sump (Owens Lake) and filled successive basins southward and eastward until it entered Lake Manly, the former body of water that covered most of Death Valley (Fig. 1). At the same time, Death Valley regularly received the discharge of both the Amargosa and Mohave Rivers, whose combined waters entered from the south, as they still do in high floods. Lake Manly, at its height, was about 160 kilometers (km) long, 10–17 km wide and 185 meters (m) deep. At this time, aquatic organisms, especially fishes, were able to move between several previously isolated basins.

It is now well established that the last pluvial age, which ended about 8,000–12,000 years ago, was followed by the warmer climate we know today. This higher average temperature caused some Pleistocene lakes to dry up entirely, while others shrank. Their large outlets withered away and only small streams remained. These small streams and the many springs dotting the landscape became refuges for remnants of the once abundant aquatic life.

Recent Hydrography

Today the entire hydrologic basin draining into Death Valley covers an area about 22,500 square kilometers (km^2) with about 1,300 km^2 of the basin below sea level (Hunt, *et al* 1966). The basin floor contains one of the world's great saltpans covering more than 500 km^2 and lying as much as 86 m below sea level. The principal surface drainage into Death Valley is the Amargosa River, with its headwaters near Beatty, Nevada, draining about 13,700 km^2 of arid desert land. The Amargosa River, despite its large watershed, is dry most of the year where it enters the southern part of Death Valley. The next largest watershed is Salt Creek, draining the northwest arm of Death Valley, an area of about 5,700 km^2. Mountains and alluvial fans draining directly into Death Valley cover an additional 3,100 km^2. Despite the enormous size of this drainage basin, little surface water is now available for aquatic organisms.

With today's arid conditions in the Death Valley region, direct precipitation within the hydrologic basin is not sufficient to account for the water discharge in several groups of major springs (Winograd and Thordarson 1975). Most springs and streams are now dependent upon underground, interbasin flow of water through permeable, carbonate rocks in order to maintain their high discharge rates. For example, major springs in the Ash Meadows area of Nevada collectively discharge more than 2,700 hectare-meters of water annually (40,125 liters per minute) from highly fractured carbonate rocks of Paleozoic age (Dudley and Larson 1976). This movement of water is collected underground from an area encompassing no less than 11,600 km^2 and includes parts of 10 intermontane valleys hydraulically connected by interbasin movement of water through the carbonate rocks. Seven of these valleys are topographically closed. The major uplands in the Ash Meadows Ground Water Basin are the Spring Mountains and the Sheep Range, both near Las Vegas, Nevada, reaching altitudes of over 3,000 m and receiving as much as 64 cm of precipitation annually. Precipitation in these mountains, however, may not be the source of the spring water. Recent studies have shown the age of water issuing from the springs to be between 8,000 and 12,000 years (I.J. Winograd, pers. comm.). Apparently this vast underground reservoir is not being recharged solely by surface precipitation as was once suspected but, rather, is a huge body of water that has existed since pluvial times. It is now slowly draining along fault lines and emerging as springs in the Ash Meadows–Death Valley area. The underground basin may be much larger than that shown in Figure 2, as available data are not yet adequate to delineate the northern boundaries of the water-bearing carbonate rocks.

The surface drainage to springs in Ash Meadows is only a few hundred square kilometers. Measured spring discharge is about 2,700 hectare-meters annually, but unmeasured evapotranspiration and possible underflow beneath the springs and into Death Valley may be an additional 1,000 hectare-meters of water annually (Dudley and Larson 1976). Discharge from various Ash Meadows springs range from a few liters per minute (lpm) to about 10,600 lpm. Hydrologists who have studied the situation agree, explicitly or implicitly, that in view of the aridity of the region, the discharge must originate beyond the small surface-watershed tributary to the springs. It has been estimated that as much as 35% of the ground water reaching Ash Meadows travels a distance of about 145 km, entering the Ash Meadows Basin from the adjacent White River Groundwater Basin north of Las Vegas (Winograd and Thordarson 1975; Dudley and Larson 1976). So far, no evidence has been found for a ground water divide between these basins. Additionally, spring discharge in and around Furnace Creek in Death Valley appears to be derived from the Ash Meadows Groundwater Basin, but other sources are also possible. Without this source

of groundwater, the fishes, other aquatic life, and many terrestrial animals would have disappeared from this region long ago.

The source of water for springs that previously existed in Pahrump Valley to the east of Ash Meadows is not definitely known. The most likely source was runoff from the nearby Spring Mountains, but a direct connection with the Ash Meadows Groundwater Basin or the White River Groundwater Basin cannot be ruled out.

Owens Valley receives its water directly from runoff from the Sierra Nevada, White, and Inyo Mountains, whereas springs along the ancient Mohave River, south of Death Valley, may originate from water derived from the San Bernardino Mountains east of Los Angeles.

HISTORY AND EVOLUTION OF FISHES IN THE DEATH VALLEY SYSTEM

God quickened in the sea and in the rivers
So many fishes of so many features
That in the waters we may see all creatures;
Even all that in the earth is to be found,
As if the world were in deep water drowned
Du Bartas, *Divine Weeks and Works.*
wk. i, day 5.

History

The fish fauna of the broadly connected Death Valley System during the late Pleistocene was probably much more abundant and diverse than it is today. Previously, there may have been temporary connections with the Lahontan System via the Owens River drainage to the north and the Colorado River, allowing a free exchange of numerous fish species. Most valleys in the Death Valley System contained lakes deeper than 50 m, connected by rivers during pluvial periods (Hubbs and Miller 1948).

The late Pleistocene terrestrial environment in the Death Valley System was characterized by moderate temperatures, less xeric vegetation, and more available water. A few plant fossils and sediment cores taken from the floor of Death Valley and other basins allow a reasonably accurate reconstruction of the late Pleistocene environment (Mehringer and Warren 1976). Mountains were rather densely vegetated with Juniper woodlands extending down to 850 m. Lakeshores graded into extensive shallow marshlands, and flows of springs, such as those in Ash Meadows, were much greater and supported large marshes. Rivers, although flowing in discrete channels, had extensive quiet backwaters and shallow sloughs.

Excellent mid-late Pleistocene mammal fossils, primarily from Lake Tecopa near Shoshone, California, reveal the presence of a diverse group of large and small mammals (Whistler 1972). There were many varieties of small rodents and numerous species of rabbits. Presumably they maintained large populations in productive marshes and grasslands. Large grazing herbivores, such as camels, horses and mastodons were surprisingly abundant, indicating ample vegetation. Predators of the numerous herbivores included saber-toothed tigers and dire wolves as well as a number of smaller carnivores.

Only four species of fossil fishes have been discovered in the Death Valley area (Miller 1945). All are members of the killifish family (Cyprinodontidae). Three of the species belong to the genus *Fundulus* and are related to modern Ash Meadows and Pahrump killifishes (Fig. 3). The fourth species is of the genus *Cyprinodon,* a pupfish. Although there is some controversy as to the age of these species, it is probable that all four occurred in early Pleistocene or late Pliocene times, about two million years ago.

It is reasonable to assume that the extensive Pleistocene waters of the Death Valley System contained numerous, larger species of fish as well as ancestors of the small modern forms. One can look at present fishes of the Colorado River, through which ancestors of killifishes and pupfishes entered the Death Valley System, for an indication of other possible types of fish life inhabiting the Pleistocene waters. Minnows and suckers, entering from the Lahonton Basin to the north, may well have existed in the Pleistocene Death Valley System.

As the climate of southwestern United States became progressively more arid between 4,000 and 10,000 years ago, many of the Pleistocene watercourses disappeared, leaving desiccated remnant habitats that are

FIGURE 3. During the less arid Pleistocene Epoch many different types of fishes inhabited the Death Valley System. The fossil killifish pictured above existed in this area millions of years ago. Fish found in this area today are different from those present in ancient times. Species, as we know them now, have evolved from other fish species like the fossil pictured above, and are still evolving. In time, today's species will gradually evolve into new species and leave their presence known only as fossils.

present today. When the lakes receded and rivers dried, the larger fish species were exterminated. In the Owens River drainage, the only portion of the Death Valley System to retain significant amounts of flowing water, species requiring abundant, cool water, such as the Owens chub *(Gila bicolor snyderi)* and the Owens sucker *(Catostomus fumeiventris),* have persisted until the present time (Miller 1973; Pister 1974). Throughout the remainder of the system, smaller fishes survived to the present in small, isolated oases of permanent water.

Evolution

Today, isolated springs and streams, remnants of the Pleistocene Death Valley System, are "islands" in a sea of desert. Just as the biological processes and resultant divergent forms of terrestrial life on the remote Galápagos Islands strongly influenced the thinking of Charles Darwin, recent studies of the aquatic islands of Death Valley have increased our knowledge of the evolution of life forms. Evidence of gradual evolution of distinct species and subspecies of pupfish and killifish in isolated springs and streams provide us with a particularly clear example of the evolutionary process (Brown and Feldmeth 1971; Turner 1974). Desert fishes are one of the few groups of species for which scientists have reasonable estimates for the length of isolation of different populations which allows measurement of natural rates of evolution.

The ancestral pupfishes were isolated at intervals over the past 12,000 to 20,000 years in the small remaining habitats. Today there are more than 20 isolated pupfish populations in the Death Valley System. These populations have evolved into 10 distinct types of pupfishes: four species and six subspecies of a fifth species (Pister 1974). Each species and subspecies has evolved distinctive shapes and markings as well as biological adaptations. Evolution and differentiation of pupfishes and killifishes in the Death Valley System has been influenced by three primary factors: stresses of the environment (selection pressure), length of isolation, and habitat and population size. These three factors are the forces driving the process of evolution.

SELECTION PRESSURE

Pleistocene pupfishes presumably inhabited shallow, interconnected lakes, marshes, and streams in which environmental parameters (temperature, dissolved gases, salinity, etc.) fluctuated both daily and seasonally. These pupfishes were probably highly variable in morphology and had the ability to withstand wide environmental extremes. Today some Death Valley pupfish populations are isolated in extremely variable environments, such as the Amargosa River and Salt Creek. Others are isolated in essentially constant temperature, stable springs, such as Devils Hole, Big Spring, and School Spring. In isolation there is no interbreeding (gene flow) between populations, setting the stage for evolution of new species. Selection pressures in the different environments have gradually altered the genetic makeup of populations by allowing those individuals best adapted to the particular stresses of isolated habitat to survive and reproduce in greater numbers. Thus, pupfish populations slowly evolved into different species and subspecies, each adapted to specific isolated habitats. The process of speciation is dynamic: environments are continually changing, and resident populations are forced to adapt or face extinction.

LENGTH OF ISOLATION

Evolutionary change is a gradual process that occurs in isolated populations. Consequently, length of isolation strongly influences the amount of differentiation between populations. Fish populations isolated for the longest periods (10,000 to 20,000 years) are either distantly removed from the center of distribution (such as the Owens pupfish [*Cyprinodon radiosus*]) or are in higher elevation, inaccessible habitats (Devils Hole pupfish [*Cyprinodon diabolis*]). These species are the most divergent pupfishes in the Death Valley System (Miller 1948). The Devils Hole pupfish is extremely divergent, both morphologically and behaviorally, as a result of long isolation under the unique and restrictive selection pressures of the Devils Hole environment. The Owens pupfish, although isolated for nearly as long, is more similar to the Amargosa pupfish *(Cyprinodon nevadensis)* because both species are isolated in separate but similar environments. On the other hand, the Amargosa pupfish has differentiated into several subspecies that have been intermittently connected, reducing the length of isolation to intermediate lengths of time, ranging from 400 to 4,000 years (Mehringer and Warren 1976).

HABITAT AND POPULATION SIZE

Population size also influences the speed and extent of differentiation. When a small population is isolated, it contains only a portion of the total variability in the parent population. This may lead to random establishment of certain characteristics that are not influenced by selection pressures in the environment (this process is known as genetic drift). Genetic drift may account for some of the extreme morphological differences present in the Devils Hole pupfish. It can also lead to rapid extinction of small populations if their inherent genetic variability is not sufficient to respond to envi-

ronmental change.

Studies of morphology, behavior, life-history patterns, physiology, and biochemistry of pupfishes in the Death Valley System reveal that the greatest differences in all characteristics exist between species isolated for the longest time periods under different environmental conditions (Brown and Feldmeth 1971; Liu 1969; Miller 1948; Soltz 1974; Turner 1974). Species differ most in morphology and least in biochemical and physiological tolerances, indicating that natural selection acts differentially on separate portions of the pupfish genome (population pool of genetic variability). Pupfishes, in general, are able to adapt to a tremendous range of physiological stresses, and even species long isolated in such restricted environments as Devils Hole have retained much of their original ability. Subspecies of the Amargosa pupfish, which have been more recently connected, are not as divergent. They show adaptive patterns strongly influenced by either variability and unpredictability (Amargosa River pupfish) or constancy and predictability of their habitats (Saratoga Springs, Ash Meadows and Warm Springs pupfish).

Like several pupfish populations, the Mohave chub and Owens chub probably have been isolated for over 20,000 years, yet are considered to differ only at the subspecific level. This limited differentiation is probably due to similar selection pressures acting on the large and variable populations in the two areas, or it may be that pupfishes evolve more rapidly than chubs and other minnows.

The speckled dace populations of the Owens and Amargosa River drainages all differ to varying degrees. Ichthyologists are studying them to determine the number of distinct subspecies in the Death Valley System. The Owens sucker, the only member of its group in the system, is distributed throughout the Owens River drainage and shows no subspecific differentiation. The Pahrump and Ash Meadows killifishes probably were isolated for over 20,000 years. Each of the three large springs in the Pahrump Valley contained a distinct subspecies that evolved in isolation of unknown duration. The Ash Meadows killifish populations were not considered to have been subspecies, indicating a shorter period of isolation of their spring habitats.

PRESENT DISTRIBUTION AND HABITATS

In the world's dreary desert a crystalline pool . . .
J. T. Trowbridge, *On Amos Bronson Alcott.*

The Fishes

In modern times the Death Valley System has been inhabited by a rather limited native fish fauna consisting of members of three families, five genera, 10 species and 11 recognized subspecies. Of the three families, the killifishes (Cyprinodontidae) have adapted most successfully to the rigorous, arid environment of the area. All but four types of Death Valley System fishes are killifishes which occur in a variety of isolated springs and stream courses. There are also three members of the minnow family (Cyprinidae) and a single sucker (Catostomidae) that are restricted to the deeper, cooler, permanently-flowing waterways. Miller, *et al* (1977) give a complete bibliography on fishes and aquatic resources of the Death Valley System, and only the major pertinent papers are cited here.

KILLIFISH FAMILY CYPRINODONTIDAE

Killifishes characteristically occur in salt, brackish, alkaline, and fresh waters throughout the temperate and tropical regions of the world. These small fishes, from 2.5 to 10 cm long, are generally minnow-like with all fins soft-rayed and pelvic fins located well back on the abdomen. However, minnows and killifishes are not closely related, and killifishes readily can be distinguished by the presence of scales on top of the flattened head, toothed mouth angled upward, and rounded or square caudal (tail) fin. Males and females usually differ in size and shape (sexual dimorphism) with the deeper-bodied males of many species becoming brilliantly colored during the breeding season (sexual dichromatism), when most are territorial.

OWENS PUPFISH
CYPRINODON RADIOSUS MILLER
Figures 4, 5

This fish, not many decades ago, was abundant in marshes, sloughs, and other slow, shallow waters along the Owens River (Kennedy 1916). Due to severe habitat loss as a result of water withdrawal from Owens Valley, the Owens pupfish was thought to have become extinct, but now is known to have survived and occurs in three protected habitats near Bishop, California (Miller and Pister 1971). It is classified by state and federal governments as an endangered species, but is making a strong recovery.

This species can be distinguished from other pupfish species in the Death Valley System by the very anterior position of the dorsal fin and higher average number of fin rays. Males are deeper bodies than females and the general color is silvery blue overlying darker lateral bars (the usual pattern for male pupfish). Breeding males become deep blue with blue dorsal and anal fins strikingly rimmed in orange. The black band on the margin of the caudal fin of breeding males is less distinct than in any other pupfish species. The elongate and round-bodied females, as is usual in pupfish, are a more drab olive-brown, with brown lateral blotches shaped like inverted teardrops and an ocellus (eye spot) on the posterior portion of the dorsal fin.

SALT CREEK PUPFISH
CYPRINODON SALINUS MILLER
Figures 6, 7

This pupfish lives only in Salt Creek, a saline stream flowing from approximately 55 to 70 m below sea level from south of Devils Cornfield toward Cottonball Marsh on the floor of Death Valley (Miller 1943, 1948). Salt Creek originates at McLean Springs and flows for four to six km on the valley floor in the spring months, but dries in mid-summer to a series of marshes extending approximately 1.5 km below McLean Springs. This is one of the harshest and most variable of the pupfish habitats in the Death Valley System.

The Salt Creek pupfish, slenderest of the Death Valley pupfishes, is covered with very small scales and has a posteriorly-located dorsal fin. As is usual in pupfish the sexes are strikingly different. The female is characteristically more elongate, brownish with a silvery

FIGURE 4. Owens pupfish (*Cyprinodon radiosus* Miller). Male above (4.0 cm Total Length), female below (3.3 cm T.L.). This species was once found over much of Owens Valley, California, but is now restricted to three sanctuaries there.

FIGURE 5. Owens pupfish. Alan Heller.

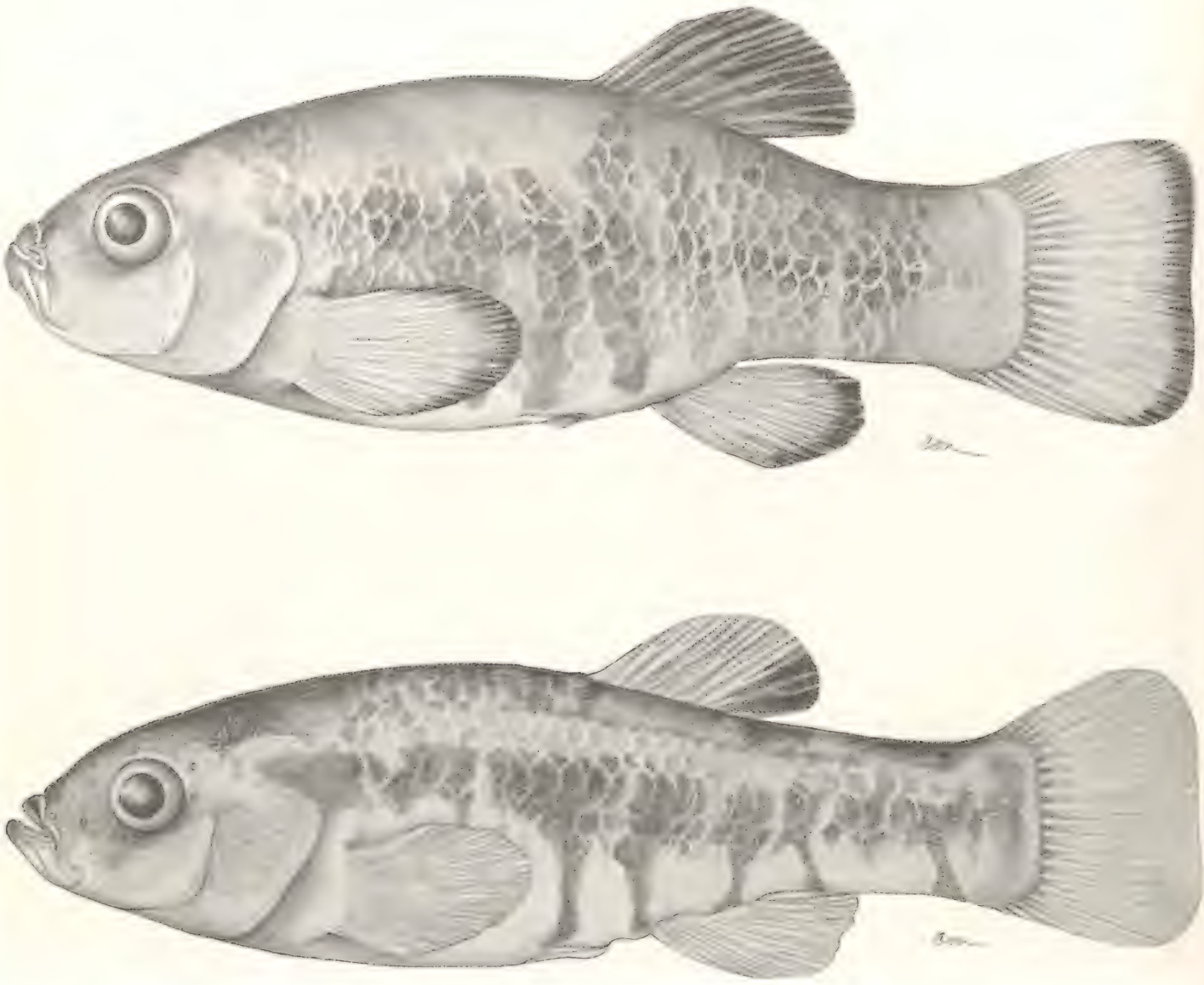

FIGURE 6. Salt Creek pupfish (*Cyprinodon salinus* Miller). Male above (4.4 cm T.L.), female below (3.6 cm T.L.). These pupfish are restricted to Salt Creek on the floor of Death Valley, California.

FIGURE 7. Salt Creek pupfish. Robert Liu.

sheen, and has the typical series of lateral blothes. Breeding males are bluish to turquoise with dark grey lateral bars, a purplish-blue sheen along the back, and an overall silvery sheen on the sides. The dorsal fin is dark grey and there is a distinct black band on the margin of the caudal fin.

COTTONBALL MARSH PUPFISH
CYPRINODON MILLERI LABOUNTY AND DEACON
Figures 8,9

This pupfish lives in the harsh and unusual environment of the Cottonball Basin, an extensive area of saltpan approximately 73 m below sea level in Death Valley (LaBounty and Deacon 1972). The saline pools and channels in which it lives may reach nearly five times the salinity of seawater. However, due to continuous flow of water from the underground aquifer and cooling effect of a high surface evaporation rate, water temperatures achieve only a rather pleasant 32°C at a scorching air temperature of 46°C (Naiman, *et al* 1973). It appears that the Cottonball Marsh pupfish inhabits a rather stable environment, now isolated only a few kilometers distant from Salt Creek.

This pupfish closely resembles the Salt Creek pupfish which is clearly its recent ancestor. The Cottonball Marsh pupfish is on the average smaller and more slender, with an even more posterior dorsal fin, and a marked reduction or complete absence of pelvic fins. Sexes are typically dimorphic and closely resemble Salt Creek pupfish in coloration. Females are somewhat distinctive in that the blotches on the sides often fuse to form a lateral band.

AMARGOSA PUPFISH
CYPRINODON NEVADENSIS
EIGENMANN AND EIGENMANN
Figures 10, 11, 12

Amargosa pupfish live in a number of isolated springs, marshes and stream courses along the Amargosa River drainage. In pluvial times (periods of greater precipitation) the ancestor of this species probably lived in all areas of the drainage except the headwaters near Beatty, Nevada. The pluvial river flowed south to Pleistocene Lake Tecopa, then west, and finally turned north to enter the southern end of Death Valley. As the climate changed and the drainage system dried up, pupfish became isolated at different times in various permanent aquatic habitats. In isolation, the ancestral Amargosa pupfish differentiated into six morphologically distinct forms recognized as subspecies (Miller 1948). Due to man's direct altering of aquatic habitats and continued pumping of water for human consumption and irrigation, all native fishes in the Amargosa River drainage are threatened and two subspecies are now thought to be extinct (Miller 1972; Pister 1974).

Although the six subspecies of Amargosa pupfish can be distinguished readily by ichthyologists, each having certain unique features, their basic shape and coloration are rather similar. The species is characterized by large, regularly-spaced scales, the dorsal fin nearer the caudal fin base than the tip of the snout, and the small pelvic fins may be lacking occasionally. All subspecies are sexually dimorphic: adult males are very deep bodied, while females are more slender and rounded in cross section. Breeding males are intense blue overlying black vertical bars, with a distinct black terminal band on the caudal fin. Females all have an ocellus at the posterior base of the dorsal fin and a nearly continuous, often very faint, series of inverted teardrop-shaped blotches on the sides. Maximum adult size is only 6.5 cm. The six subspecies are:

SARATOGA SPRINGS PUPFISH
CYPRINODON NEVADENSIS NEVADENSIS

This subspecies is found only in Saratoga Springs in the southeastern corner of Death Valley National Monument. The habitat is a rather constant temperature spring (26.5–29°C), and its overflow forms a series of marshes and shallow lakes (Deacon 1967, 1968). While breeding adults are most readily seen in the spring pool, literally millions of young pupfish are in the lakes by early summer. Limited studies indicate that while the young may leave the spring pool, no pupfish move from the lakes into the springs.

This subspecies is the type from which the species was described in 1889, by Dr. C.H. Eigenmann of Indiana University and is the first pupfish described from Death Valley. Male Saratoga Springs pupfish have the deepest and broadest body and, while breeding, the most intense blue coloration of all the subspecies.

AMARGOSA RIVER PUPFISH
CYPRINODON NEVADENSIS AMARGOSAE MILLER

This pupfish occurs in two permanent flows of the lower Amargosa River in California but is absent from its headwaters near Beatty, Nevada. One population lives in the river flowing from Tecopa through the Amargosa Canyon. Below the canyon the river water dissipates into the sand near Dumont Dunes, a distance of 9–12 km. The other population inhabits a short permanent flow approximately 1.6 km long in Death Valley northwest of Saratoga Springs. These habitats are harsh and extremely variable, being subject to flash floods in winter and extreme desiccation during summer. The two flows may be connected during rare periods of heavy rain when the Amargosa River flows continuously for nearly 50 km from well above Tecopa to

Death Valley (Soltz 1974).

The two populations have differentiated only slightly and are characterized by the highest scale counts of any of the subspecies and tend to be more elongate and streamlined (though not nearly so much so as the Salt Creek pupfish). Breeding males have a silver sheen over an intense blue background color. Females are often very drab olive-brown with faint lateral blotches.

TECOPA PUPFISH
CYPRINODON NEVADENSIS CALIDAE MILLER†

This subspecies formerly occurred in the outlets of North and South Tecopa Hot Springs and probably in two or three other nearby springs on the terrace on the north side of Pleistocene Lake Tecopa. These habitats were apparently separated from the Amargosa River by small but impassable waterfalls. The Tecopa pupfish is now believed to be extinct due to habitat alteration (public baths on the spring sources at Tecopa Hot Springs) and hybridization with the Amargosa River pupfish which now occupies the terrace due to man's alteration of the waterfall barriers (Pister 1974).

This pupfish subspecies is distinguished from the Amargosa River pupfish by its much larger scales. In color patterns it was similar to the Amargosa River pupfish.

SHOSHONE PUPFISH
CYPRINODON NEVADENSIS SHOSHONE MILLER†

This subspecies is considered extinct. It formerly lived in a few slow flow "holes" along the swiftly flowing outlet of Shoshone Spring at Shoshone, California. Even at the time of its first collection in 1939, the restricted habitat was highly disturbed (Miller 1948). The source pool was known as "Squaw Hole" because it served as a laundry area for local Indians. Also much of the spring flow is often diverted into a concrete swimming pool. These disturbances probably led to the extinction of the Shoshone pupfish which was perhaps last seen in 1966 (Miller, R.R., pers. comm.).

The Shoshone pupfish was very similar to the Tecopa pupfish but could be distinguished by its slender body and slab-sided appearance.

ASH MEADOWS PUPFISH
CYPRINODON NEVADENSIS MIONECTES MILLER

The Ash Meadows pupfish occurs in at least eight of the largest springs in Ash Meadows, Nevada. Their habitats are relatively large (4.5 to 24 m in diameter and 2 to 9 m in depth) and relatively warm with constant temperatures (ranging from 24 to 30°C). All springs inhabited by Ash Meadows pupfish are at elevations of 655 to 700 m and are distributed along an irregular north-south contour line for a distance of about 16 km. All of these habitats are threatened by severe reduction of spring flows due to excessive water pumping by a recent large-scale agricultural operation in Ash Meadows (Deacon and Bunnell 1970). The Ash Meadows pupfish population in Jackrabbit Spring was extirpated in 1969 when the spring was drained by a pump suspended directly over the spring source. At least two other populations (in Crystal Spring and Forest Spring) may have been eliminated by the combined effects of severe habitat alteration and introduction of exotic fishes.

The Ash Meadows pupfish is characteristically short, deep, slab-sided, and long-headed with a strongly arched nape. The fin-ray and scale counts average low for the species. Breeding males become strikingly iridescent silver-blue, and are distinctly yellowish-olive along the back anterior to the dorsal fin.

WARM SPRINGS PUPFISH
CYPRINODON NEVADENSIS PECTORALIS MILLER

The Warm Springs pupfish lives in seven, small, warm springs within an area of less than 2.6 km^2 at about 710 m elevation on the west slope of the unnamed hills containing Devils Hole in Ash Meadows, Nevada (Miller and Deacon 1973). Its habitats are all small; the spring pools are less than 2 m in diameter and 1.3 m deep, and some flows have no source pool at all. All of the springs, except Mexican Spring, are warm and maintain constant temperature (range 30 to 33°C). Mexican Spring, the smallest known pupfish habitat, dried in 1973, due to habitat alteration (Soltz 1974). Due to small size and local distribution of the springs inhabited by the Warm Springs pupfish, the subspecies is listed as endangered.

The Warm Springs pupfish is the smallest of the subspecies and can be distinguished from the other forms by its shorter, deeper body and more numerous pectoral fin rays. It also shows the strongest tendency toward reduction and loss of pelvic fins. In coloration, breeding males are similar to the Ash Meadows pupfish, with the yellow on the nape being so pronounced as to be readily seen by observers.

DEVILS HOLE PUPFISH
CYPRINODON DIABOLIS WALES
Figures 13, 14

This species exists as native only in Devils Hole which lies in a detached portion of Death Valley National Monument in Ash Meadows, Nevada. Devils Hole is located at 732 m elevation in a 15 m depression along a fault on the side of an unnamed hill in central

FIGURE 8. Cottonball Marsh pupfish (*Cyprinodon milleri* LaBounty and Deacon). Male above (4.2 cm T.L.), female below (3.7 cm T.L.). These pupfish are only found in parts of Cottonball Marsh, nearly 80 m below sea level, on the floor of Death Valley, California.

FIGURE 9. Cottonball Marsh Pupfish, female. Alan Heller.

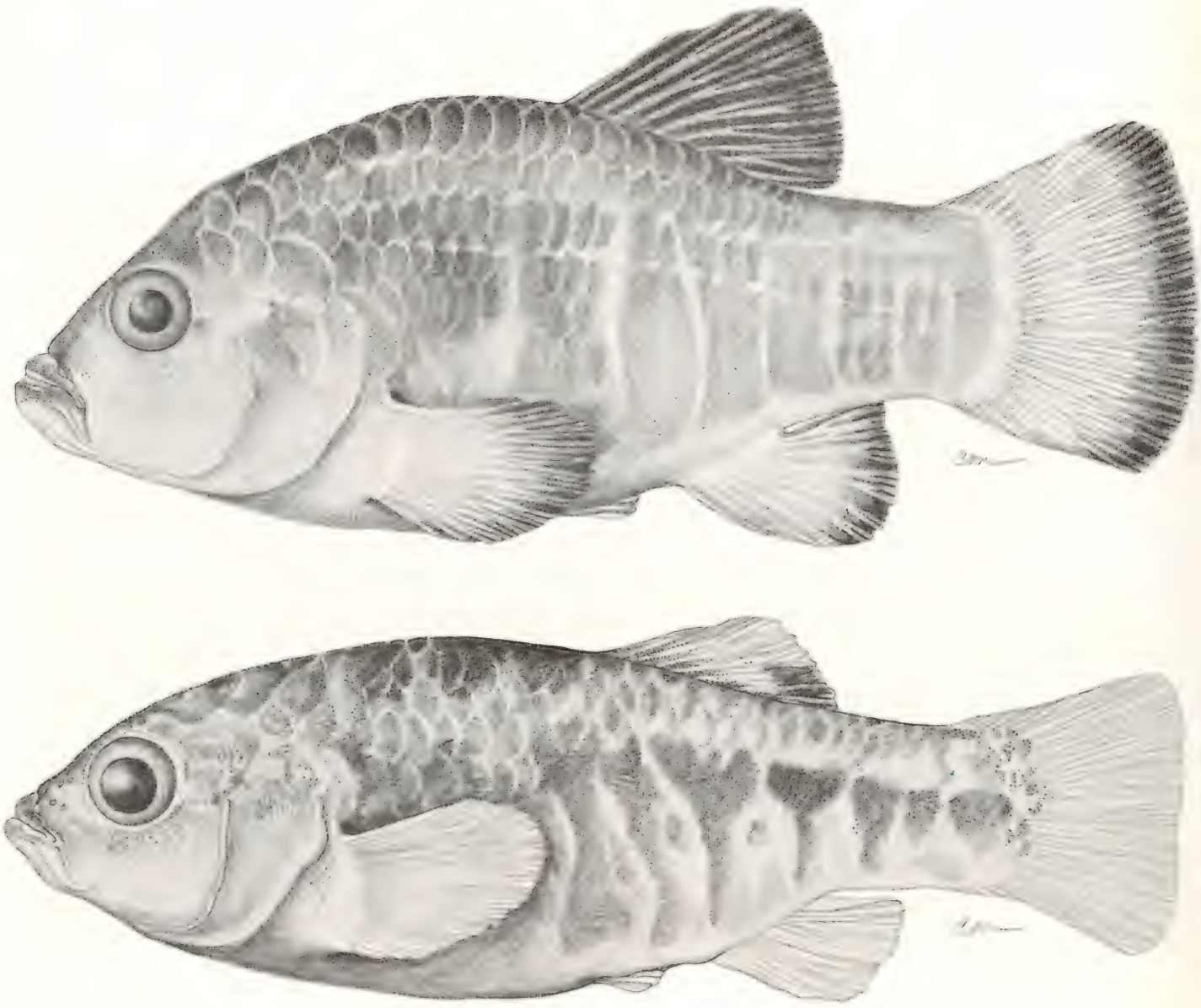

FIGURE 10. Amargosa pupfish (*Cyprinodon nevadensis* Eigenmann and Eigenmann). Male above (3.8 cm T.L.), female below (4.3 cm T.L.). Amargosa pupfish are found throughout the Amargosa River, Ash Meadows, Nevada, and in Saratoga Springs, Death Valley National Monument.

FIGURE 11. Male Amargosa pupfish. Alan Heller.

FIGURE 12. Female Amargosa pupfish. Alan Heller.

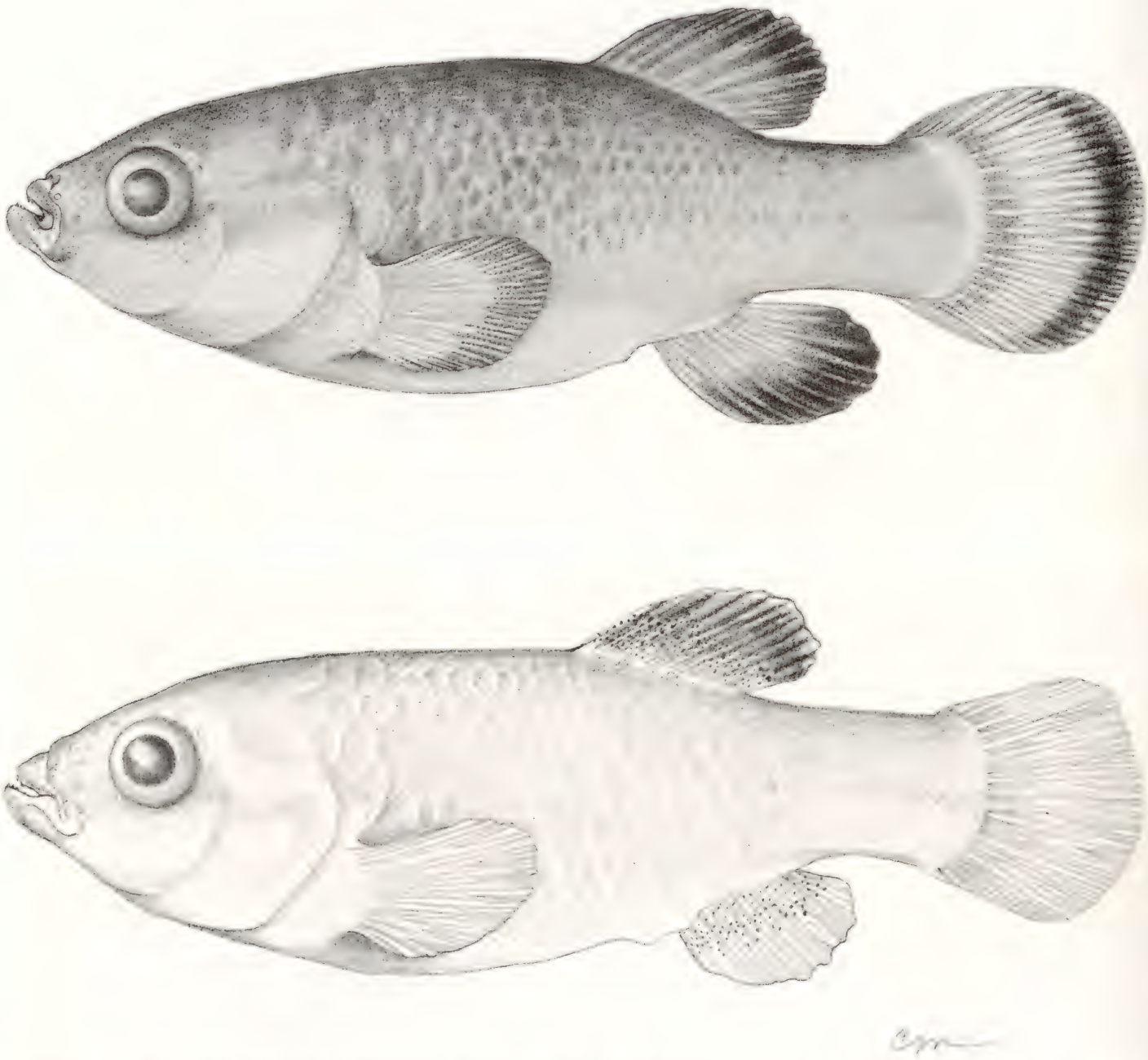

FIGURE 13. Devils Hole pupfish (*Cyprinodon diabolis* Wales). Male above (2.7 cm T.L.), female below (2.3 cm T.L.). Found only in Devils Hole, Ash Meadows, Nevada.

FIGURE 14. Devils Hole pupfish. Alan Heller.

Ash Meadows (Wales 1930). Although the Devils Hole pool is the head of a vast underground water system, the pupfish depends on a shallow limestone shelf for both food and spawning area (James 1969). Persistent lowering of the water level in the early 1970's, due to pumping for irrigation, gradually exposed the shelf, seriously reducing the critical pupfish habitat and rapidly threatening the survival of the Devils Hole pupfish (Pister 1970, 1971). Legal proceedings, including a ruling by the U. S. Supreme Court, specify that pumping must be curtailed to allow constant coverage of enough of the shelf to maintain a stable population (Sanchez 1976). This species, however, is still in a very precarious situation and remains listed as endangered. As an additional precaution a population of Devils Hole pupfish has been established in an artificial refugium below Hoover Dam.

The Devils Hole pupfish probably has been isolated longer than any other Death Valley System pupfish (a reasonable estimate is 10,000 to 20,000 years). It has undergone significant evolutionary change during this long period of isolation and is remarkably distinct from its closest relative, the Amargosa pupfish. It is the smallest of the some 25 species of pupfish, rarely exceeding 2.5 cm in length, and has retained a number of features (large head and eye, long anal fin, reduced pigmentation) characteristic of juvenile pupfish. Pelvic fins are completely lacking, as are vertical bars in either males or females. Females lack the ocellus on the dorsal fin. Breeding males become solid silver-blue and show the characteristic black terminal band on the caudal fin.

PAHRUMP KILLIFISH
EMPETRICHTHYS LATOS MILLER
Figures 15, 16

This species formerly existed in three springs and their separate drainages in isolated Pahrump Valley, Nevada. In the past each spring flowed strongly and maintained a constant temperature of approximately 24.5°C. Killifish from each spring were slightly different and have been described as three separate subspecies (Miller 1948, 1950). Unfortunately, pumping water for irrigation resulted in the desiccation of virtually all springs. As a result, two subspecies are now extinct (Minckley and Deacon 1968). The habitat of the third subspecies became completely dry during the summer of 1975. Biologists, anticipating this tragedy, had already transplanted Pahrump killifish into three separate refuge sites. As a result, one subspecies survives today, but not in its native Pahrump Valley.

All three subspecies are characterized by an elongate body with dorsal and anal fins placed far back on the body, complete lack of pelvic fins, broad upturned mouth, and sides with a dark longitudinal streak. Dorsal, anal and caudal fins are a bright orange-yellow and there is an orange ring around the eye. Females are larger and greenish-brown with conspicuous black mottling. Males are smaller and silver-blue, without mottling.

MANSE RANCH KILLIFISH
EMPETRICHTHYS LATOS LATOS

This subspecies exists only in refugia outside Pahrump Valley. Manse Spring, its only habitat, went dry in 1975.

RAYCRAFT RANCH KILLIFISH
EMPETRICHTHYS LATOS CONCAVUS MILLER †

Extinct. Raycraft Spring, the only habitat of this subspecies, was bulldozed and closed in 1955, wiping out the entire population.

PAHRUMP RANCH KILLIFISH
EMPETRICHTHYS LATOS PAHRUMP MILLER †

Extinct. Pahrump Spring, the only habitat of this subspecies, went dry between 1955 and 1957. What had been the largest Pahrump killifish population was completely gone when scientists discovered the destruction of its habitat.

ASH MEADOWS KILLIFISH
EMPETRICHTHYS MERRIAMI GILBERT †
Figure 17

This *extinct* species, only thirty years ago was present, although rare, in most of the large springs in Ash Meadows that also contain Ash Meadows pupfish (Miller 1948; Minckley and Deacon 1968). Apparently, competition and predation by exotic fishes have exterminated all populations of this unique fish species. The last specimen was seen in 1948.

The Ash Meadows killifish was basically similar to the Pahrump killifish but could be distinguished by its narrower mouth and a mottled dark color pattern, rarely forming a lateral line. Unfortunately, we know virtually nothing of its breeding color, behavior, or natural history.

MINNOW FAMILY
CYPRINIDAE

The minnow family is the largest of all freshwater fish families. Its distribution is worldwide except for Australia and surprisingly, South America. There are approximately 250 species in North America, including carp, chubs, dace and shiners. Minnows, technically,

are not just small fish, they form a natural group possessing many common characteristics: all fins are soft-rayed; caudal fin is forked; head is scaleless; pelvic fins are located on the abdomen; teeth are absent on the jaws, but specialized ones are present in the throat. Most minnows are small (under 15 cm long) but the Colorado squawfish *(Ptychocheilus lucius),* reaches a length of 2 m. Minnows are exclusively freshwater fishes, with low salinity tolerance, that typically live in moderately fast-flowing water or in ponds and lakes of some depth. Consequently, few species were able to survive the great restriction of habitats and increasing salinity and alkalinity as the aquatic environment decreased with development of arid conditions in the American Southwest over the past 10,000 years. Only three species of minnows now survive in the Death Valley System.

SPECKLED DACE
RHINICHTHYS OSCULUS (GIRARD)
Figures 18, 19

This extremely variable minnow is widely distributed over the western United States and occurs in many isolated drainages in the Great Basin. It lives in a wide variety of habitats from swift, cool, mountain streams to warm, lowland rivers and even desert warm springs. These isolated populations have undergone some adaptation to differing environments but generally the changes are subtle and most populations in the Great Basin are not assigned to separate subspecies (Hubbs, *et al* 1974). In the Death Valley System speckled dace occur in a few tributary streams of the Owens River; in the headwaters of the Amargosa River where they are the only native fish; in the Amargosa Canyon near Tecopa, California, but not in the flow in Death Valley itself; and in most of the large springs in Ash Meadows that also contain Ash Meadows pupfish.

Speckled dace can be distinguished from other minnows in the Death Valley System by their slightly overhung snout, dark lateral stripes often running the entire length of the body, speckles and splotches on the sides, small fins, and small size (rarely over 8 cm long). The various isolated populations differ in degree of speckling and completeness of the lateral stripe. Breeding males develop fleshy bumps (nuptial tubercles) on the rays of the pectoral and anal fins that are used during spawning.

OWENS CHUB
GILA BICOLOR SNYDERI MILLER

This subspecies of the tui chub *(Gila bicolor)* formerly abounded in Owens Valley, but now is isolated in a section of the Owens River near Bishop, California. Although chubs are still abundant throughout Owens Valley, most are hybrids between the native Owens chub and other subspecies introduced as bait minnows by anglers. The only remaining pure population of Owens chub is located in a spring-fed flow in the old river channel in Owens Gorge north of Bishop (Miller 1973). There it is isolated from all other water due to the water appropriation project of the City of Los Angeles, which carries much of the Owens River in a pipe from Long Valley Dam to Pleasant Valley Reservoir. This is perhaps the only case of water withdrawal from a drainage system having actually resulted in the perpetuation of a native fish. However, this one restricted population is far from secure and, as a result, Owens chubs have been further introduced into the Owens Valley Native Fish Sanctuary.

As its scientific name implies, this species is bicolored, being dusky-olive above and whitish below. The upper surface has gold highlights, particularly on the head.

The Owens chub is completely isolated from the other subspecies of tui chub in the Death Valley System, the Mohave chub, described below. The two subspecies can be separated by the very different gill raker number and by a number of subtle features including fewer pelvic and anal fin-rays and a more distinct bicolored pattern in the Owens chub (Miller 1973).

MOHAVE CHUB
GILA BICOLOR MOHAVENSIS (GIRARD)
Figure 20

This subspecies, which evolved in isolation in the Mohave River, has now completely hybridized with the arroyo chub *(Gila orcutti)* that was introduced into the river over 40 years ago (Hubbs and Miller 1943). Three pure populations of Mohave chub remain in highly modified habitats at Soda Springs (formerly known as Zzyzx Springs) on the southeast shore of Soda Dry Lake, near Baker, California. Because of its restricted distribution, the Mohave chub is listed as endangered by both the state and federal government. In hopes of insuring its survival, the Mohave chub has been transplanted into a number of fishless but permanent waters in the desert area and also into some artificial habitats near Los Angeles.

Although similar to the Owens chub, the Mohave chub can be distinguished by its more numerous gill rakers and the indistinctly bicolor pattern, grading from a gold highlighted olive above to silvery white below.

SUCKER FAMILY
CATOSTOMIDAE

This family is closely related to the minnows, but differs dramatically, as the name implies, in having a sucking mouth with fleshy, papillae-covered lips on the

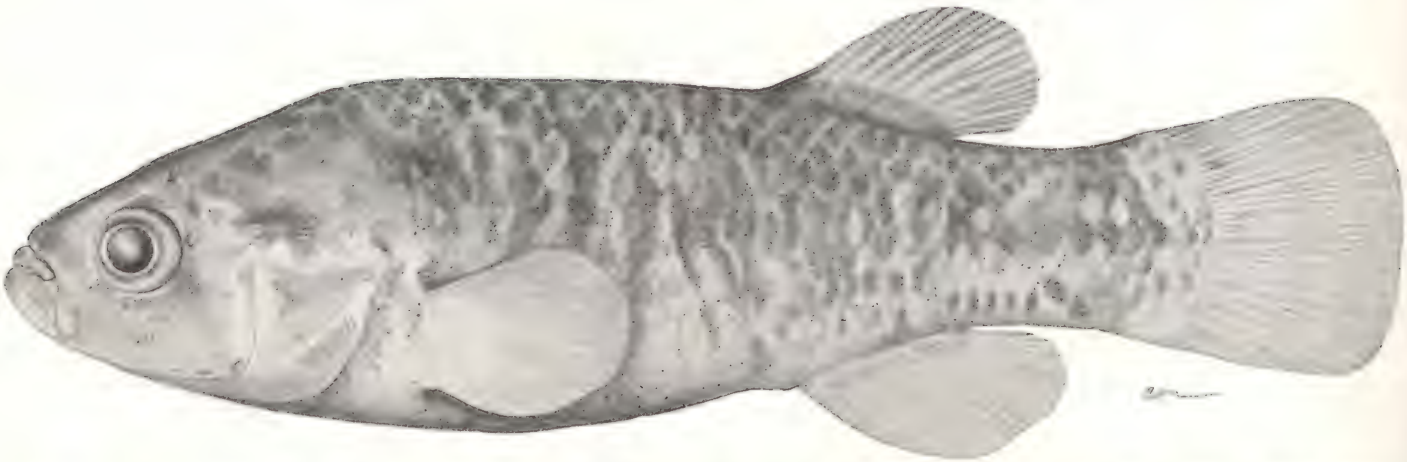

FIGURE 15. Pahrump killifish (*Empetrichthys latos* Miller). Sexes are similar but females may be slightly more mottled. Native to springs in the Pahrump Valley, Nevada. Two of the three subspecies are extinct and the third subspecies is endangered. Drawn from specimen 6.0 cm T.L.

FIGURE 16. Pahrump killifish. Douglas Selby

FIGURE 17. Ash Meadows killifish (*Empetrichthys merriami* Gilbert)†. Sexes are similar in appearance but females may be slightly more mottled. This species is now extinct and was restricted to large springs in Ash Meadows, Nevada. Drawn from specimen 5.0 cm T.L.

FIGURE 18. Speckled dace (*Rhinichthys osculus* [Girard]). Sexes are similar in appearance. Speckled dace are found in the Owens Valley, the Amargosa River, and springs in Ash Meadows, Nevada. Drawn from specimen 5.7 cm T.L.

FIGURE 19. Speckled dace–Owens Valley form. Alan Heller.

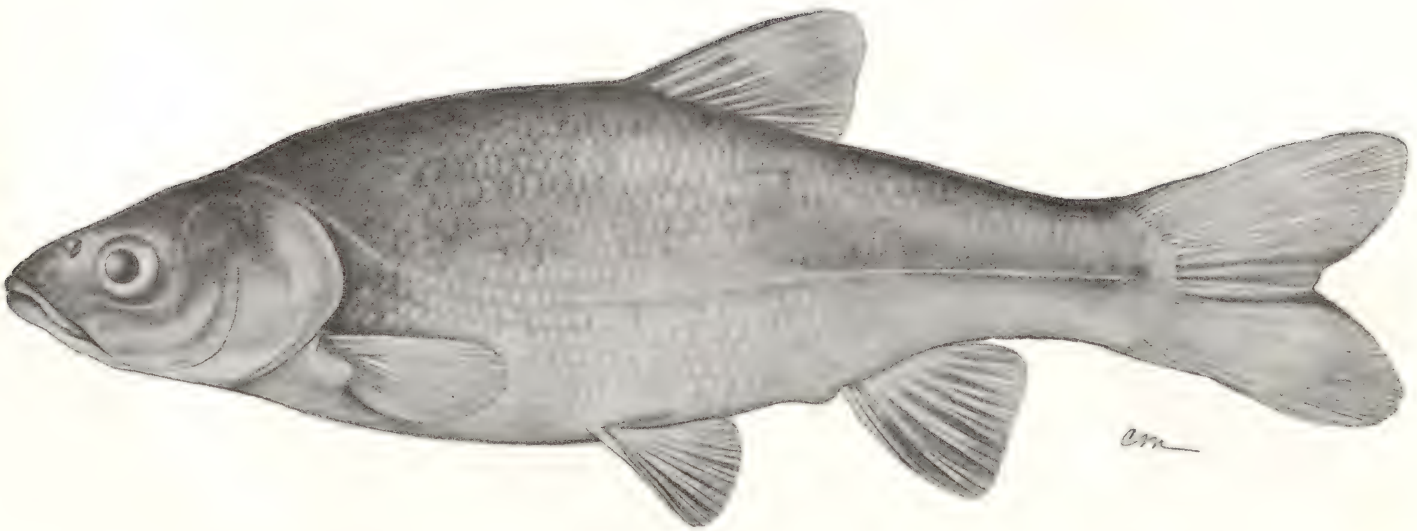

FIGURE 20. Mohave chub (*Gila bicolor mohavensis* [Girard]). Sexes are similar in appearance. Drawn from specimen 12.4 cm T.L. Presently restricted to Soda Springs south of Death Valley, near Baker, San Bernardino Co., California. A related subspecies, the Owens chub *(Gila bicolor snyderi),* is similar to the Mohave chub and is found only in Owens Valley, California.

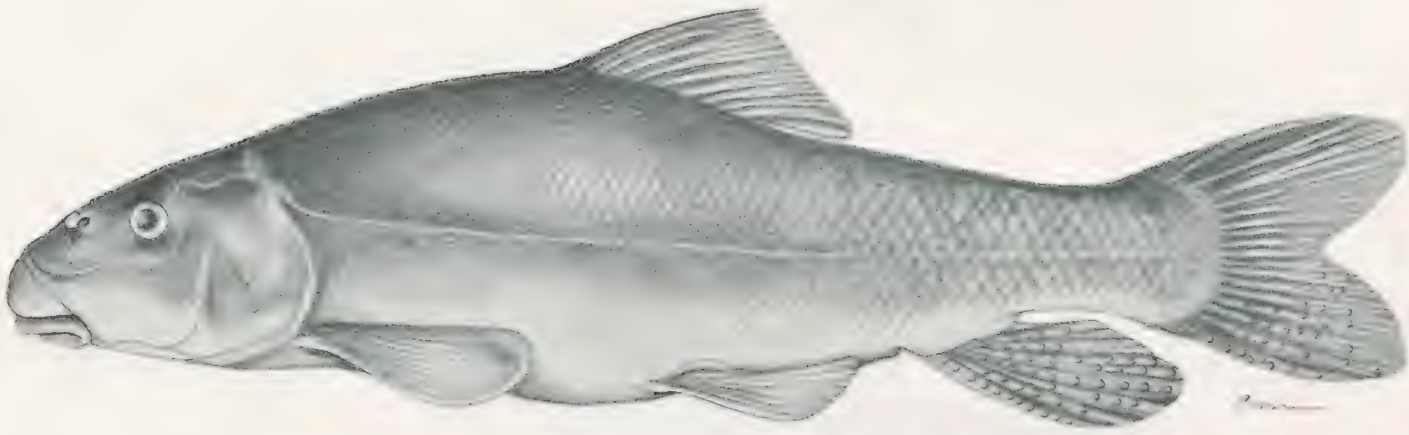

FIGURE 21. Owens sucker (*Catostomus fumeiventris* Miller) Male (22.6 cm T.L.). Sexes are similar in appearance. Found throughout the Owens Valley, California.

FIGURE 22. Owens sucker. E.P. Pister.

underside of the head. The family is almost completely restricted to the fresh waters of North America, where about 80 species occur. There are two species in Asia. Suckers are typically larger than minnows and have been even less successful in surviving and evolving in the shallow, warm, saline waters of the Death Valley System. The one sucker in the system is restricted to the Owens River drainage, the least arid portion of the entire system.

OWENS SUCKER
CATOSTOMUS FUMEIVENTRIS MILLER
Figures 21, 22

The Owens sucker is abundant throughout the flowing waters and shores of reservoirs of most of the Owens River drainage. It occupies the total range of available habitat types although it is most common in pools at the ends of riffles over gravel bottoms. Among the native fishes of the Death Valley System, this species seems to have been least affected by man's activities.

The Owens sucker can be readily distinguished from all other native fishes in the system by its ventral sucking mouth. The fish is almost entirely slate-gray and the only obvious difference between sexes is a faint bluish cast on breeding males (Miller 1973). The Owens sucker is moderately larger than other native fishes reaching a length of at least 40 cm.

The Habitats

Although the Death Valley System is today a desiccated remnant of former extensive Pleistocene waterways, remaining isolated aquatic habitats are a significant component of the desert ecosystem. The many varied habitats each contain unique types and assemblages of fishes as well as other aquatic and terrestrial organisms. The Death Valley System now consists of four isolated drainages (Fig. 23). Miller, *et al* (1977) gives a complete bibliography of aquatic resources of this area.

The most extensive drainage is the Amargosa River with its associated, but isolated, spring systems in Ash Meadows, Nevada, on the margins of Pleistocene Lake Tecopa, and at Saratoga Springs in the southeastern corner of Death Valley. Also, the extremely isolated Pahrump Valley may have had a past connection with Ash Meadows as determined by geologists and reflected in the occurrence of closely related killifishes in both areas (Miller 1948, 1950; Hubbs and Miller 1948).

The Amargosa River flows for three short stretches: from its headwaters near Beatty, Nevada, through the Shoshone-Tecopa area and the Amargosa Canyon, and in the southern end of Death Valley west of Saratoga Springs. The Mohave River now normally ends at Soda Lake, about 65 km south of Death Valley. Another system consists of Salt Creek and Cottonball Marsh on the open floor of Death Valley. These two isolated habitats were connected until about 2,000 years ago, a very short period in geological time. The Owens River is furthest from Death Valley and has been isolated longest. Historically it terminated at Owens Lake which is 160 km and two mountain ranges west of Salt Creek.

Fishes surviving in the isolated portions of the Death Valley System have undergone evolutionary change producing unique adaptations to their particular habitats. What are these desert aquatic habitats like? How do they differ and what types of desert fishes occupy the different habitats? How do these desert oases influence vegetation, wildlife, and man? These questions cannot be answered completely, but much is known about aquatic habitats in the Death Valley System and the complex communities they support. Each of the four drainages is considered separately.

AMARGOSA RIVER DRAINAGE

The headwaters of the Amargosa River are near the old mining town of Beatty, Nevada. Underground waters draining from Pahute Mesa Groundwater Basin to the north strike impermeable sediments forcing water to the surface where it flows for a few kilometers (Winograd and Thordarson 1975). The elevation is about 1,100 m, and the local combination of moderate temperature and sizeable stream flow have allowed development of relatively lush streamside vegetation, including willows and cottonwoods not commonly found along desert streams in the Death Valley area. The current is moderately swift and the stream consists of riffles and occasional large pools. This habitat is ideal for speckled dace, which are the only native fish in the headwaters. Dace may be seen in schools feeding on drifting insects in riffle areas. These small minnows are common, and although not well studied, population size numbers in the hundreds of thousands in late summer and is presently little affected by man's activities.

The relatively high elevation and steep gradient of the headwaters, with attendant seasonal floods, probably kept pupfish, which swim poorly in swift currents, from colonizing the upper reaches of the Amargosa River. The Amargosa River disappears into permeable sands of the Amargosa Desert about 4 km south of Beatty where its channel is normally dry for more than 80 km.

The Amargosa River again reaches the surface on the impermeable clays of the dry bed of Lake Tecopa.

Existing Springs and Streams Containing
Native Desert Fishes
SPRINGS
STREAMS
INTERMITTENT STREAMS
MARSHES
0 10 20 miles
0 10 20 30 40 km
FISH SLOUGH
Bishop
WARM SPRINGS
OWENS RIVER
INYO MOUNTAINS
SIERRA NEVADA
Saratoga Flats
Beatty
NEVADA
AMARGOSA MOUNTAINS
PANAMINT MOUNTAINS
PANAMINT VALLEY
DEATH VALLEY
SALT CREEK
COTTONBALL MARSH
ASH MEADOWS
AMARGOSA RIVER
PAHRUMP VALLEY
MANSE SPRING
SHOSHONE
TECOPA
SARATOGA SPRINGS
N
W
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S
CALIFORNIA

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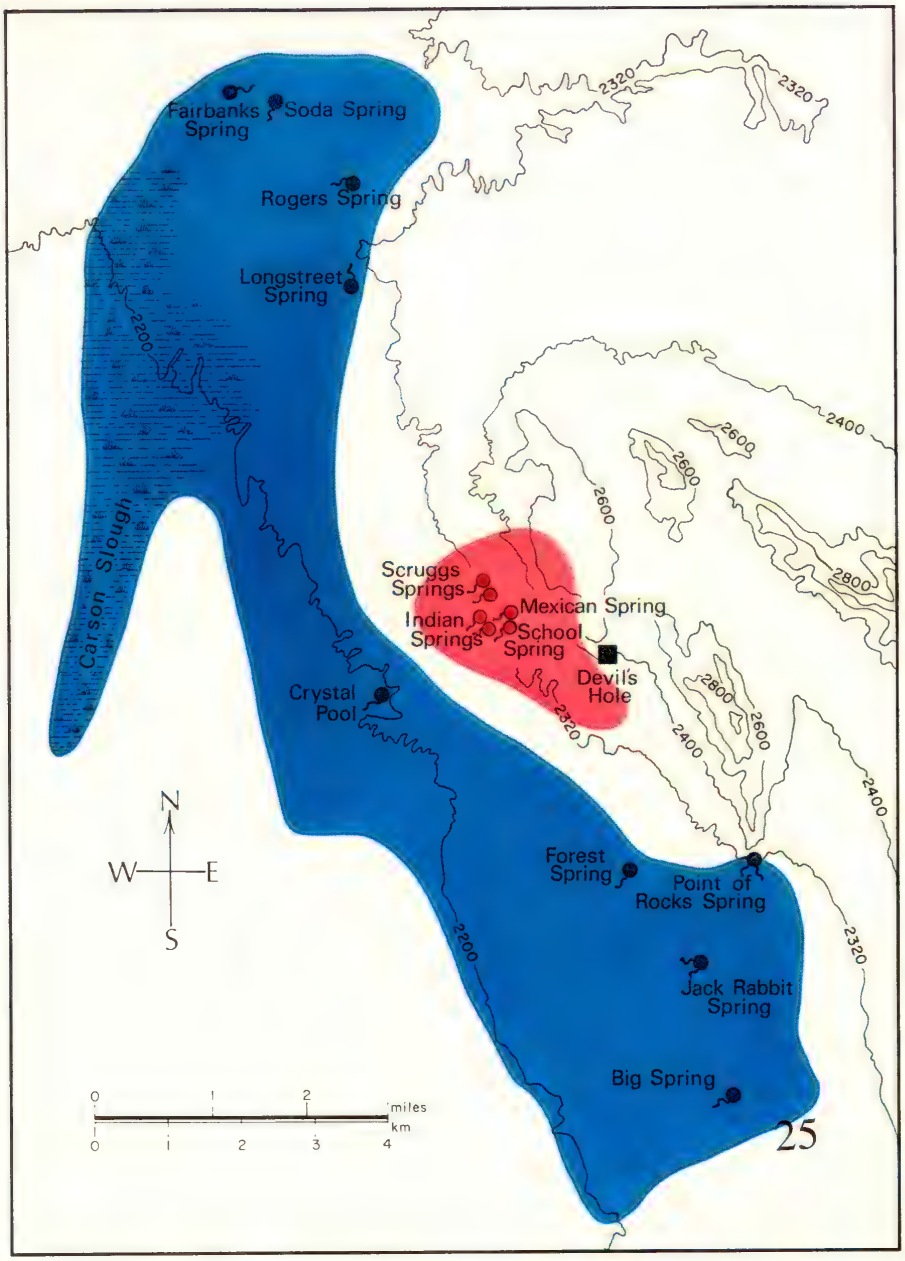

FIGURE 23. Fish species in the Death Valley System are widely scattered. Location of extant native fish populations are shown on the map and the names of springs, marshes and streams are given.

FIGURE 24. Amargosa Canyon near Tecopa, California. Robert Naiman.

FIGURE 25. Numerous springs and fishes occur in Ash Meadows, Nevada. During the Pleistocene Epoch a large lake may have covered this area or the spring flows may have been substantially larger and connected with the Amargosa River. In either case, as the region became drier, the once connected fish populations became isolated in spring groups according to elevation. The highest spring and the one isolated first was Devils Hole. Pupfish occurring here *(Cyprinodon diabolis)* have undergone the greatest evolutionary change. The next highest group of springs was isolated later (in red) and the pupfish here *(Cyprinodon nevadensis pectoralis)* have evolved differently than those pupfish isolated in lower springs (in blue, *Cyprinodon nevadensis mionectes*).

There it flows slowly through a series of continuous tule marshes until it enters the rocky gorge of Amargosa Canyon (Fig. 24). Here, the gradient steepens and the river flows in a distinct channel. After flowing for 10 or 12 km the stream again sinks into permeable sands where the canyon opens into Sperry Wash near Dumont Dunes. The dry river channel curves west and turns north to enter the south end of Death Valley. There, isolated by about 32 km of desert, water comes to the surface one final time and the river flows for only about 1.6 km on the floor of Death Valley.

The Amargosa River pupfish is present throughout the lower Amargosa River. Although the two habitats are isolated by 32 km of dry desert, the pupfish populations are nearly identical in form and ecological adaptations (Miller 1948). Ecologists feel they are identical adaptive types that have evolved to meet similar severe environmental stresses. Water temperatures in the river vary from near freezing in winter (ice actually may form on shallow, quiet water) to temperatures of over 40°C in midsummer. Because of extremely high summer air temperatures, evaporation greatly reduces river flow, drying many side pools and shallow areas. Consequently, thousands of fish are killed by physical stress or are taken by avian predators which feed heavily on these concentrations of weakened and dying fishes. Periodic heavy winter rains and resultant flash floods ravage the habitat. Flood waters may reach depths of over 2 m in Amargosa Canyon where the river is normally less than 0.3 m deep. Such tremendous floods scour the habitat and flush thousands of fish downstream into the normally dry stream bed where they perish as the waters quickly recede. In response to these environmental stresses, the reproductive ecology of Amargosa River pupfish has evolved to allow an overwintering population of a few tens of thousands to rapidly increase to millions by early summer (Soltz 1974).

Two other fish species live in the Tecopa–Amargosa Canyon area. They are an endemic population of speckled dace and an introduced and, unfortunately, well established population of mosquitofish *(Gambusia affinis)*. Their absence from the Amargosa River in Death Valley suggests virtually complete isolation of that habitat. Although an extremely severe flash flood could conceivably flush fish from Amargosa Canyon to habitat in Death Valley, any fish that may have survived such a journey have not become established. Only the remarkable pupfish has managed to survive throughout the entire lower Amargosa River drainage. Although speckled dace are common in Amargosa Canyon, they are not now as abundant as in the headwater habitat, possibly because of competition with pupfish. Also the mosquitofish population is rather small, indicating its tenuous survival in the river and, hopefully, minimal competition with the two native fishes.

The entire river, particularly in Amargosa Canyon, provides a rare and beautiful desert oasis for all forms of life. Rocky ground and shading by the steep gorge walls have facilitated development of particularly lush streamside vegetation. There are dense stands of willows, groves of mesquite, and during spring months, many species of water-loving wildflowers. Water and streamside vegetation are essential for many of the terrestrial animals found in the area. A recent biological survey indicates that more than 100 species of birds, 40 species of amphibians and reptiles, and 20 species of mammals utilize the area (Sully, *et al* 1972). The Amargosa River, particularly in the gorge, is a complex and fragile desert ecosystem largely isolated from surrounding desert terrain.

The Amargosa River and associated vegetation and wildlife have supported man in the Death Valley area for millenia (Sully, *et al* 1972). Sleeping circles, campfire sites, and primitive tools supply abundant evidence of early Indian cultures along the lower river. Anthropologists have established the presence of four different Indian cultures in Amargosa Canyon, probably extending back 10,000 years. The canyon influenced development of the Death Valley area by European man. A portion of the Old Spanish Trail from Santa Fe to Los Angeles passed through the canyon. This route was traveled by the 49'ers, Kit Carson, bands of cattle rustlers, and hundreds of prospectors. Remnants of the now defunct Tonopah and Tidewater Railroad can still be seen in the canyon.

Ash Meadows, Nevada is located 9 to 15 km east of the dry bed of the Amargosa River at Death Valley Junction. In this area of about 160 km^2 between the Amargosa Desert and unnamed hills on the east, subterranean water, gathered over millenia from thousands of square kilometers of Great Basin desert, issues from the earth. The Meadows, as it is locally known, contains several dozen springs and seeps, at least 20 of which contain native fishes. Three species, and two subspecies of a fourth species, occur here. Only one other arid region of North America, the Cuatro Ciénegas Basin in the Chihuahuan Desert of east-central Mexico, can match this diversity of springs and endemic fishes (Minckley 1969).

The evolutionarily significant association between fish fauna, and spring elevation and size is illustrated in Figure 25. Eight large, lower elevation springs (Big Spring, Crystal Spring, etc.) contained Ash Meadows pupfish, speckled dace and Ash Meadows killifish (now extinct). These springs probably have had the shortest period of isolation. At a slightly higher elevation, there are seven or eight smaller, warmer springs concentrated in an area of less than 2.5 km^2 (Fig. 26). These springs contain only one species of fish, the Warm Springs pupfish. Although they occasionally may be connected, these springs have probably been

separated from the lower elevation springs for at least several hundred years.

Devils Hole is located at the highest elevation (730 m) on the side of a hill in central Ash Meadows (Fig. 27). The pool lies 15 m below the surface of the earth in a fault fracture, has no surface outlet, and is the hydrostatic head of a vast underground aquifer (Fig. 28). Devils Hole has been isolated from surface waters for 10,000 to 20,000 years. Not surprisingly, the Devils Hole pupfish, which has evolved in probably the most restricted and isolated habitat of any fish in the world, is vastly different from all other pupfish.

Ash Meadows is a large and lush oasis in one of the most arid regions of the world. Consequently it supports a great diversity of plant and animal life dependent on regular availability of water. The vertebrate fauna of the area is not as well studied as that of Amargosa Canyon but there are many varied forms of life in each area. The flora of the area is well known. Ten species of flowering plants are endemic to Ash Meadows and at least 20 more plants are found there and in only a few other oases in the Mohave Desert, including the variety of velvet ash *(Fraxinus velutina* var. *coriacea)* for which the area was named (Beatley 1971).

The beauty, fascination, and biological value of this desert oasis cannot be measured adequately. Tragically, many fish populations are threatened by introduced exotic species and the entire water-supported ecosystem in Ash Meadows has been severely disrupted by recent large-scale agricultural developments. These threats to Ash Meadows, and to the entire Death Valley System, and what is being done about this situation are discussed in the chapter on conservation of desert fishes.

Ash Meadows is rich with artifacts of past Indian cultures. Although less well studied, the history of Indian occupation may be as extensive as that of Amargosa Canyon. One legend, still passed on by local residents, tells of an Indian maiden who cast herself into Devils Hole and whose skeleton later appeared in Big Spring, 9 km to the south. More reliable accounts concern the regular use of Devils Hole as a gathering place by prospectors. The local name of "Miner's Bathtub" comes from this tradition (Halliday 1955). Although Ash Meadows never had a large resident population, clay and peat mining between 1910 and 1930 brought enough people to support a one-room school near School Spring.

About 50 km south of Ash Meadows numerous springs arise along the Amargosa River near Tecopa, California. One such isolated spring is located near Shoshone, California. It has no spring pool and flows down a steep gradient into a marsh along the Amargosa River. The only pool habitat along the flow, known locally as "Squaw Hole," was used by Indians for centuries (Miller 1948). Today the spring flow is used to irrigate a football field and to fill a community swimming pool. Continual disturbance by man and recent added pressure of competition with exotic fishes have caused the extinction of the Shoshone pupfish.

Nearby, at Tecopa Hot Springs, a series of small springs arise on a shoreline terrace of Pleistocene Lake Tecopa about 30 m above the present flow of the Amargosa River. These springs issue from the ground at temperatures near 44°C. The Tecopa pupfish, though rarely moving upstream to temperatures above 37°C, was found in all of the spring outflows, hottest of pupfish environments (Miller 1948). As a result of development of public and private baths on all spring heads and radical alterations of their outflows, this pupfish is now considered to be extinct. Amargosa River pupfish are now present in the lower reaches of these springs, having moved up from the river when natural waterfall barriers were removed during development.

Saratoga Springs, another isolated spring system in the Amargosa River drainage, are located at the southeastern edge of Death Valley National Monument about 2.5 km from the last flowing section of the Amargosa River. Water flows from the base of the Ibex Hills via one 10 meter-diameter spring and three smaller ones. The warm water (27 to 29°C) flows into a six-hectare marsh containing one temporary lake and one permanent shallow lake (Fig. 29). The marsh is dammed by stabilized sand dunes on its north and west margins. Presumably, in times of greater spring discharge, these dunes were breached and the spring flow connected with the Amargosa River (Mehringer, P.J., pers. comm.).

The first pupfish described from Death Valley was collected from Saratoga Springs in 1881 (Eigenmann and Eigenmann 1889). The Saratoga Springs pupfish is now known to be a distinct subspecies, occurring only in the main spring pool and the overflow marsh and lakes. Significant differences between this subspecies and the Amargosa River pupfish indicate a relatively long period of isolation by the intervening sand-dune dam.

Saratoga Springs is well known to naturalists. Many wayward waterfowl land on the lakes. More than 150 species of birds are recorded from the area. At least 15 species of reptiles and amphibians and 18 species of mammals also occur about Saratoga Springs (Deacon 1967, 1968).

Natural vegetation is a treeless tule marsh. Until recently, introduced tamarisk trees of three species provided shade for weary desert travelers and aided in stabilizing the sand dunes containing the marsh. They were removed by the National Park Service in 1972 because their roots extracted large amounts of water, which evaporated from their leaves. Since their removal, the level of the spring has risen several centimeters,

FIGURE 26. School Spring, Ash Meadows, Nevada. Robert Naiman.

FIGURE 27. Devils Hole, Ash Meadows, Nevada. David Soltz.

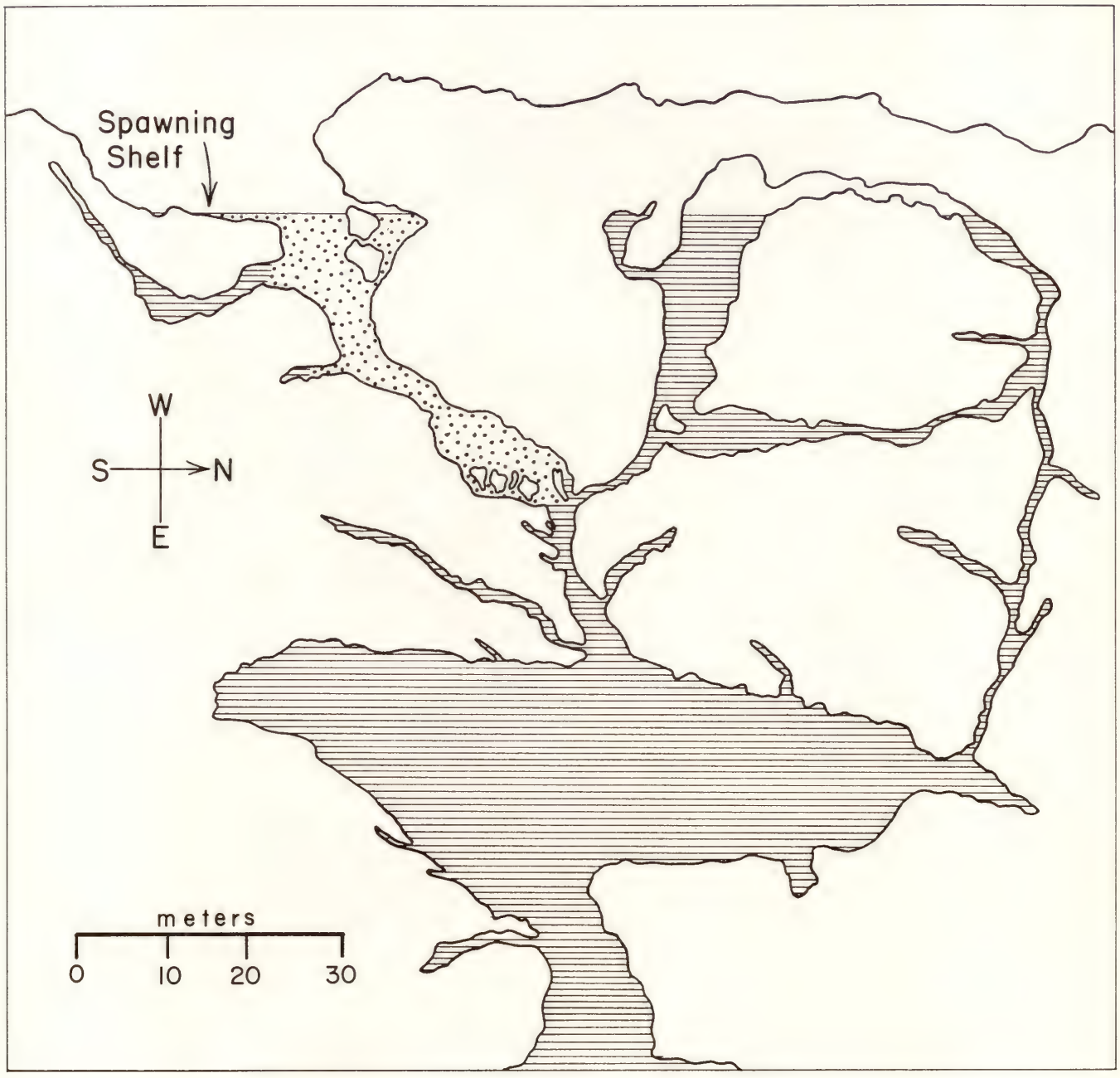

FIGURE 28. Devils Hole is a large, water-filled, limestone cavern in Ash Meadows, Nevada. Exploration by divers over the last 25 years has allowed a cross-section of the cavern to be mapped. There are several large rooms and the depth is at least 100 m. Total depth and extent of the cave is not known but it is obviously much larger than the portion already explored. The Devils Hole pupfish are found only near the mouth of the cave in the vicinity of the rock shelf but will venture to depths of 26 m (stippled area). (Courtesy of J.E. Deacon).

creating additional habitat for pupfish and other aquatic organisms (Sanchez, P.G., pers. comm.).

Indian sites at Saratoga Springs and nearby hills have provided anthropologists with the best continuous record of primitive man in the Death Valley area. Here, as in Amargosa Canyon, there is good evidence of four different Indian cultures; the Saratoga Springs culture existed from approximately 1 AD to 1000 AD (Wallace and Wallace 1978). Saratoga Springs was also a critical watering spot for prospectors. Later attempts were made to develop the springs into a mineral bath resort. Now the habitat is protected and has been returned to near pristine condition by the National Park Service.

PAHRUMP VALLEY

Pahrump Valley is a moderate-sized, internal drainage basin on the western edge of the Spring Mountains. The valley is presently separated from Ash Meadows to the northwest and the rest of the Amargosa River drainage to the south and west by hills ranging from only 45 m to over 800 m in elevation above the valley floor.

Numerous warm springs arise along the margins of the valley floor. Three large springs, completely isolated although located within 11.5 km of each other, were inhabited by slightly different subspecies of the Pahrump killifish (Miller 1950). Each constant temperature spring (24.5°C) and the more variable outflow environments and irrigation ditches contained large populations of killifish. Unfortunately, all Pahrump killifish habitats have gone dry due to excessive ground water pumping and extreme modification of springs for agricultural development in the valley. Two of the three subspecies have been extinct for over 20 years (Minckley and Deacon 1968). The habitat of one subspecies, Raycraft Spring, was filled by bulldozing in 1955, and that of the other, Pahrump Spring, went dry between 1955 and 1957. The third subspecies, Manse Ranch killifish, is now maintained in three refugia outside Pahrump Valley. Its only habitat, Manse Spring, was a large (10 m in diameter), densely vegetated spring with a flow of over 0.03 cubic meters per second, was pumped completely dry in June, 1975.

MOHAVE RIVER DRAINAGE

The headwaters of the Mohave River, Deep Creek and small tributaries, drain the north slopes of the San Bernardino Mountains east of Los Angeles. Once out of the mountains the river sinks into permeable sands and flows intermittently through much of its course eastward and then northward toward Death Valley. Several perennial springs that persist along the river course support fish and other aquatic life. The final flow of the river is through Afton Canyon northeast of Barstow, providing a small oasis for desert wildlife. The northernmost waters of the Mohave River drainage are Soda Springs on the southwest shore of Soda Dry Lake, about 65 km south of Death Valley.

A single native species of minnow, the Mohave chub, once flourished in all permanent, lower elevation waters of this drainage (Snyder 1918). Now only one known genetically pure population persists, this being in Soda Springs and ponds developed from their outflow. All other Mohave chub populations have hybridized with the arroyo chub *(Gila orcutti)* introduced from coastal drainages of southern California (Hubbs and Miller 1943). Although Soda Springs is completely isolated from other Mohave River surface waters, the habitat was highly disturbed by proprietors of a large spiritual resort which operated there until 1971. The area has now reverted to the control of the Bureau of Land Management and the resort is being converted into the Mohave Desert Research Station by the California State University system. Presently, the Mohave chub is being carefully studied to determine the life history and physiological adaptations of this endangered desert minnow. Knowledge gained from studies on the Soda Springs ecosystem will aid in protecting and preserving both the fish and the spring ecosystem on which it depends for survival.

SALT CREEK AND COTTONBALL MARSH DRAINAGE

Salt Creek lies in the northern half of Death Valley, where groundwater comes to the surface at McLean Springs below Devils Cornfield at the north end of the Salt Creek Hills (Hunt, *et al* 1966). Here surface waters have cut a small canyon about 2.5 km long (Fig. 30). The flow continues below the canyon for another 1 to 3 km during spring months, when discharge is greatest and evaporation is minimal. Salt Creek does not flow out of the canyon in mid-summer due to evaporation and in many years becomes dry to within 1.0 km of McLean Springs.

Permanent habitat of the Salt Creek pupfish is McLean Springs and a series of marshes and slow-flowing pools within the canyon. These waters support dense growths of several species of semi-aquatic plants, such as salt grass, pickleweed, sedges, and cattails. Below permanent water there is little streamside vegetation, and the last 1.5 km of the streambed is devoid of flowering plants even when inundated with water. The Salt Creek pupfish is the only fish in this stream.

During spring months Salt Creek pupfish rapidly colonize the newly available downstream habitat. The pupfish population increases from a winter low of a few thousand individuals to hundreds of thousands in the

29

30

FIGURE 29. Saratoga Springs, Death Valley National Monument. Alan Heller.

FIGURE 30. Salt Creek, Death Valley National Monument. David Soltz.

FIGURE 31. Cottonball Marsh, Death Valley National Monument. Alan Heller.

four or five months each year when the habitat expands and productivity increases many fold. Shallow, downstream waters abound with juvenile pupfish; while most reproduction occurs in deeper, permanent pools. Salt Creek pupfish are so abundant during spring months that they were once utilized by the Panamint Indians as food (Miller 1948). Quantities of the fish were gathered in large porous baskets using "tule" brooms. The contents were then baked with the fish lying between layers of tule reeds alternating with layers of hot ashes. This practice apparently has been discontinued for two or more generations.

Although Salt Creek water is too mineralized for man to drink, McLean Springs forms an important watering place for large desert mammals. Tracks of coyote, kit fox, and possibly desert bighorn are present in several well worn trails leading to the springs from the surrounding desert. McLean Springs were also used by the 49'er party and innumerable prospectors' burros.

Approximately 2,000 years ago, a shallow lake extended southward across the middle basin of Death Valley from lower Salt Creek and covered Cottonball Marsh. Uplifting of the Salt Creek Hills, increasing aridity, and the resultant decrease in spring flows desiccated the lake and directed the flow of Salt Creek more easterly, cutting off the surface connection between Salt Creek and Cottonball Marsh (LaBounty and Deacon 1972).

Presently, Cottonball Marsh consists of about 260 hectares of surface water with a modest groundwater discharge estimated at 44 liters per second (Hunt, *et al* 1966). Cottonball Marsh pupfish live in a series of permanent pools and channels on the barren salt pan (Fig. 31). This fish was discovered in the late 1950's when a geologist studying the Cottonball Basin happened across its restricted habitat. Due to the isolation and fragility of this remarkable habitat, the National Park Service has chosen not to develop the area.

The Cottonball Marsh pupfish exists only in this restricted habitat on the barren floor of the hottest and driest desert in North America. It is able to survive by living in the small but permanent spring flows. Air temperatures commonly reach 48.5°C and a salinity of 160 parts per thousand (five times more saline than the ocean) has been recorded in one shallow pool. Cottonball Marsh pupfish avoid extremes of temperature and salinity by living in permanent pools and flowing channels where water temperatures do not exceed 36°C and salinity does not exceed 45 parts per thousand (Naiman, *et al* 1973). Although these pupfish frequently enter shallow pools to forage for food they retreat to permanent flowing water when environmental conditions become stressful.

The environmental stresses on Cottonball Marsh and Salt Creek pupfishes differ markedly. Salt Creek is much more thermally and ionically variable than Cottonball Marsh. It appears that these very different environmental selection pressures have caused the highly adaptable pupfish to evolve into two different species in the remarkably short time of less than 2,000 years.

OWENS RIVER DRAINAGE

The present Owens River drainage in Owens Valley, California, no longer has a surface hydrologic connection with other waters of the Death Valley System. Melting snow in the Sierra Nevada sends dozens of permanent tributaries into the Owens River. Abundant groundwater supplies the headwaters of the river and many springs along the valley floor. Historically the Owens River followed a winding course with many oxbows and shallow, marshy areas for over 125 km to Owens Lake.

Three of four native fishes of the drainage lived in tributary streams and the Owens River (Pister 1974). The Owens chub and Owens sucker inhabited flowing water of the river and its larger tributaries. Chub lived primarily in quiet pool habitats and spring-fed sloughs, while the sucker was most abundant in riffles over gravel bottoms. The second and smaller minnow, the speckled dace, preferred smaller tributaries and spring flows. The fourth species, the Owens pupfish, generally avoided fast flowing water but was abundant in springs, marshes, and shallow sloughs.

Removal of Owens Valley water through the Los Angeles aqueduct, beginning in 1910, drastically altered the aquatic habitats (Heinly 1910). Marshes and sloughs were drained or markedly reduced in area, spring flows declined, and the river was channelized and dammed. These radical habitat alterations, along with the establishment of exotic, largely predatory fishes, have had a very detrimental effect on three of the four native fishes. Only the Owens sucker remains abundant and relatively unaffected by man's activities. The Owens chub is now restricted to a small, isolated section of the old river channel in Owens Gorge below Long Valley Dam, and the speckled dace persists in a few small springs and streams. The Owens pupfish, thought to be extinct at the time of its description in 1948, survives in two refugia in Fish Slough (Fig. 32), the only large spring fed marsh remaining in the valley, and at Warm Springs refugium.

FIGURE 32. Aerial view of Fish Slough north of Bishop, California. E.P. Pister.

FIGURE 33. Conceptualized above is a typical underwater view of a spring pool habitat. In the foreground, male pupfish are courting and displaying on their territories as an interested female enters the area preparing to spawn. A young male pupfish is defending a sub-optimal territory to the left and feeding on algae growing on the spring wall. Small groups of females and juveniles forage outside the male territories and females enter only when ready to lay eggs. In the background, a speckled dace streaks by near the surface. Notice the absence of other large animals such as crayfish and frogs. They are not native to this area and severely disrupt spring ecosystems when introduced. All other native animals in springs, such as snails and crustaceans, are generally small and inconspicuous.

NATURAL HISTORY, BEHAVIOR, AND ECOLOGY

Nature does nothing in vain (Natura nihil agit frustra)
Sir Thomas Broune, *Religio Medici*. Pt. i, sec. 19.

Life History and Behavior

Field studies of pupfish from Death Valley and other areas in the arid American Southwest reveal many basic similarities in behavior and natural history. However, populations from different types of habitats show unique adaptations that have increased fitness in each particular environmental situation. The general pattern of social and reproductive biology, as well as specific unique adaptations, are well understood for pupfishes and, to a lesser extent, for the other fishes in the Death Valley System.

REPRODUCTIVE BEHAVIOR

The typical pupfish social system is based on male spawning territories (Liu 1969). During the breeding season, males vigorously defend territories comprising vertical or horizontal substrates suitable for spawning. The spawning substrate is generally a loose mixture of mud, sand, and detritus on which the eggs are laid. All pupfish populations spawn over an extended period of seven or eight months, typically from February to September. In warm springs some individuals breed throughout the year. Spawning is limited primarily by water temperature, occurring between 18 and 35°C. Consequently the peak of the daily spawning cycle shifts from mid-day to early morning and back with seasonal temperature change (Barlow 1958, 1961; Soltz 1974).

After an initial establishment phase, territories are stable and most defense is by aggressive display rather than by actual combat. In most habitats, territories are closely packed, due to a limited area of suitable spawning substrate and an excess of mature males. A receptive female swims into the spawning area and enters the territory of an actively patrolling male (Fig. 33). Normally the male pursues her, whereupon she swims toward and nips the substrate. Substrate nipping is the standard releaser of spawning behavior in pupfish, and spawning follows the chase with little or no courtship. The pair, side by side, move together a short distance along the bottom (Fig. 34). This sequence ends with simultaneous jerking during which one or occasionally two eggs are released and fertilized. Although this spawning behavior can be repeated a few times in quick succession, the female usually leaves the territory immediately after a single spawning act. Lasting pairs are not formed; rather, both sexes spawn frequently with different individuals, and there is no parental care of any kind.

Although breeding territoriality is the primary form of pupfish social organization, three other types of social systems are exhibited by pupfish populations in the Death Valley System. Each modified social system is correlated with a particular suite of environmental conditions that decrease the advantage of having a territorial breeding system (Soltz 1974). Territoriality occurs in habitats with a limited amount of suitable spawning area such as the large springs in Ash Meadows. There males must compete for the limited spawning area, and less aggressive individuals are excluded from the densely packed territorial areas. As a result, only the most aggressive and colorful males breed. Two immediate adaptive functions of breeding territoriality in pupfish are the protection of fertilized eggs of territorial males and the presence of an area for uninterrupted spawning (Echelle 1973; Soltz 1974).

Modified social systems occur in environmental situations where advantages of breeding territoriality are greatly reduced or absent. In the flowing water, variable-temperature habitats of the Amargosa River and Salt Creek, pupfish form schools and loose aggregations, wherein spawning occurs with little or no courtship. A few of the largest and most aggressive males reoccupy territories in defensible areas along the edge of the current when water temperature exceeds

18°C. However, the two main advantages of breeding territoriality do not pertain in this environmental situation. Foraging pupfish of all sizes and sexes continually enter the territories, and territorial males almost continuously chase intruders. Frequently such pursuits lead into the current, leaving the territory unguarded. Territorial males here are so highly aggressive that they seldom spawn. It appears that the high level of aggression necessary to defend a territory in the very limited, shallow side area is maladaptive. Territorial areas are ephemeral and frequently become completely dry during hot summer months. Thus, a selective advantage may go to those individuals spawning in many areas rather than in one territory, maximizing the probability of some eggs being deposited in areas that do not go dry. In both the Amargosa River and Salt Creek localities there are areas of permanent, pool-type habitat near the headwaters where territories with stable boundaries are more common. Pupfish social organization is highly responsive to the local environmental situation. Table 1 presents the various Amargosa pupfish social organizations and the environmental condition in which they occur.

TABLE 1. Amargosa pupfish social organization and associated environmental conditions.

LOCALITY	HABITAT TYPE	SOCIAL ORGANIZATION
Amargosa River	Flowing stream; variable temperature; limited and ephemeral breeding substrate.	Primarily loose aggregations in which spawning occurs; a few territorial males.
Big Spring	Large spring; constant temperature; limited, permanent breeding substrate.	Breeding territoriality.
Mexican Spring	Very small spring; variable temperature; very limited total substrate.	Monarchistic dominance hierarchy.
Indian Spring	Small spring; constant temperature; limited breeding substrate.	A few territorial males; and loose size-dependent dominance hierarchy.
Marsh Spring	Small spring; constant temperature; very limited breeding substrate.	Monarchistic dominance hierarchy; occasionally two territorial males.

A third social system is a dominance hierarchy existing in the smallest springs (Mexican Spring and Marsh Spring). This social organization may be attributed to alteration of the territorial system in confined habitats at high population density. In these small springs the individual recognition necessary for establishment of a hierarchy is possible. The hierarchies are characterized by one dominant male tyrant and a number of subordinates of approximately equal status. One dominant male controls, as his territory, the entire habitat of Mexican Spring and another, the entire spawning area of Marsh Spring. Aggressiveness of reproductive male pupfish in small springs evidently leads to a tyrant dominated hierarchy.

The most distinct social system of any pupfish studied is displayed by the Devils Hole pupfish. Males of this species are totally non-aggressive and exhibit no territorial behavior of any kind (James 1968; Liu 1969). Pairs spawn throughout the restricted suitable habitat, with very little courtship and no interference from other individuals. Absence of aggression in this pupfish species appears to be an evolutionary adaptation to thousands of years of isolation in the energy-deficient and habitat-limited environment of Devils Hole. In strong contrast, pupfish as a group are characteristically highly aggressive.

The poorly known life histories of the other species of fish in the Death Valley System are presently being investigated. The Pahrump killifish, which is in the same family as the pupfish, has similar reproductive ecology. Spawning season begins in January and extends through July, with a peak in April. Males are not territorial, and there is no parental care. Females spawn several times during the extended breeding season (Selby, D., pers. comm.)

The three species of minnows and the Owens sucker have more distinct seasonal spawning periods. Although these four fishes have been studied very little, all are known to spawn during spring and early summer (Pister, E.P., pers. comm.). Speckled dace spawn relatively small (1 mm in diameter) adhesive eggs over a gravel bottom. Breeding male speckled dace develop

orangish coloration on the anal fin base and lower caudal lobe. They have tubercles, used in mating behavior, on the pectoral fins. Some female dace may spawn twice a year. The Mohave chub and Owens chub spawn in aggregations in quiet water and broadcast adhesive eggs over the bottom. Breeding males of both species become a golden color, but lack obvious nuptial tubercles. The Owens sucker also spawns in aggregations and broadcasts large, heavy eggs over gravel substrate in flowing water. Breeding males may have rosy colored sides and develop large nuptial tubercles on the anal and caudal fins.

FOOD AND FEEDING BEHAVIOR

Fishes of the Death Valley System, as a group, are ecological generalists, and as such, have the ability to withstand a broad range of environmental variables. The natural history of these fishes clearly indicates the necessity of generalized habits for survival in the often extreme and variable desert aquatic habitats. Diets of these fishes are also highly generalized. All species of pupfish are opportunistic omnivores that take food particles, both plant and animal, in approximate proportion to their frequency in the habitat, although some species seem to prefer animal matter (Deacon 1967, 1968; Naiman 1975). The other fishes in the system are also omnivores, the diet of each species tends to emphasize either plant or animal matter, depending upon its mouth structure and specialized feeding behavior.

All pupfishes feed primarily on the substrate. Typically, a fish takes a mouthful of algae or bottom material and vigorously chews it, expelling most material through the mouth or gill covers. These feeding movements appear to be non-selective for particular food items. In a more elaborate feeding movement, after taking a mouthful of bottom material, the fish drops its body against the bottom and vigorously swims in place expelling bottom material in all directions. Then the fish turns and makes several snapping movements in the suspended bottom material. Presumably this behavior, known as plowing, allows the fish to selectively take organisms dislodged from the bottom. In addition to bottom material, pupfishes in flowing water habitats selectively feed on drifting food particles.

Feeding territories are often defended by pupfishes in habitats with large algae-free areas of bottom and minimal current (Soltz 1974). Non-reproducing adults of both sexes temporarily defend feeding territories, consisting of small pits dug by the fish repeatedly plowing in the same location. The entire algae-free bottom of a habitat may be pock-marked by pits. Less than 25 percent of the pits are occupied by pupfish at any one time. Foraging individuals frequently stop to plow and feed in abandoned pits and quickly move on. A high level of activity, consisting of feeding and charging intruders, is characteristic of pupfish defending feeding territories. Amargosa pupfish have never been observed defending a feeding territory for more than 15 minutes; most pits are spontaneously abandoned, presumably when the food supply is exhausted. High energetic demands of maintenance and low food density on feeding territories may explain their ephemeral nature.

Most non-reproducing adults and juveniles feed in loose aggregations, ranging widely through the habitat. Fry (recently hatched young) do not form foraging aggregations, although they normally congregate in the shallowest areas to feed, and perhaps to avoid cannibalism by adults. Reproductive male pupfish, on established breeding territories, feed predominantly within their territories and do not dig pits. Stomach analysis indicates reproductive males rarely consume eggs they presumably have fertilized. In fact, a function of pupfish territoriality must be the prevention of a male's offspring (fertilized eggs) being consumed by other fishes in foraging aggregations.

The main foods of omnivorous pupfishes are algae and detritus (organic material on the bottom of the habitat). The amount of algae in the diet varies seasonally, being highest in spring and summer months when algae production is high. Detritus may contribute some food energy but the major proportion of calories is extracted from the rich microbial coating on detritus particles. Pupfishes consume a large amount of detritus each day, pass it quickly through the gut, and apparently digest the microbes. Animal matter, consisting of aquatic insects, crustaceans, snails, and eggs, is also consumed by all pupfish species but the amount and type of animal matter in the diet varies both with seasonal availability and habitat. Amphipods, ostracods, and insect larvae are common in all pupfish diets during the spring months when these food species are at peak abundance. At this time, pupfish stomachs often are full of one or two species of invertebrate and very little algae, suggesting selective feeding on high protein animal matter. In contrast, snails, with their large undigestible shells, are commonly eaten only in winter when other plant and animal food is scarce. Pupfish from Saratoga Springs eat more animal food, throughout the year, than do pupfish from Tecopa Bore, a high temperature stream with a low diversity of invertebrates. Clearly pupfishes are opportunistic feeders with a selective preference for high-protein animal food when it is available.

Feeding behavior of the Ash Meadows killifish is unknown and little work has been done on the Pahrump killifish. Stomach analysis of both species indicate an omnivorous diet containing a large percentage of animal food. Large numbers of snails in the stomach and presence of heavy teeth in the throat of these killifishes indicate they are partially specialized as snail eaters.

FIGURE 34. Pupfish spawn on the bottom, laying only one egg at a time. In spring pools this follows an elaborate courtship display that is often lacking in stream and marsh populations. The male sidles up to the female, wraps his anal fin around her gonopore and fertilizes the egg as it is extruded. No parental care is involved after the egg is fertilized. Females will spawn several to many times each day, not necessarily with the same male.

Speckled dace feed in small schools foraging primarily on the bottom. Bottom dwelling invertebrates are the main food as indicated by stomach analysis, feeding behavior, and the downward directed mouth. Some drifting insects are taken in mid-stream and, at times of low invertebrate food availability, algae are taken. Dace are opportunistic, particulate feeders, typically taking the most abundant food species (e.g. insect larvae in spring months, crustaceans in fall, large amounts of algae and detritus in winter).

Both the Mohave chub and Owens chub forage in large schools, using their relatively large terminal mouth to feed on drifting insects and other invertebrates in mid-stream. Mohave chubs have a greater number of fine gill rakers, suggesting that they "filter feed" on micro-invertebrates to some extent. Both chubs also take bottom invertebrates and, when animal food is scarce, algae and detritus.

Owens suckers forage over the bottom in schools, using their fleshy, tubercled lips to scrape algae from rocks. Their lips are highly efficient at removing the fine film of algae and diatoms that normally cover rocks in streams. Microscopic crustaceans that abound in the algal film are also important food items supplying a large percentage of protein. Suckers on occasion use the fleshy lips to extract insect larvae from the substrate. Detritus is seasonally a common component of the diet. This omnivorous species exhibits dietary preferences clearly reflected by its mouth structure and feeding behavior.

Population Dynamics, Growth, and Production

POPULATION SIZES

Population sizes and densities vary according to the type of habitat. The smallest and least dense populations often occur in springs, whereas streams and marshes have large populations, which become extremely dense during warmer months. The relatively small populations in springs are largely due to limited space resulting in highly developed and structured social systems where the degree of competition between individuals is maximized. In the unpredictable environments of streams and marshes, competition between individuals is minimal, and much of the energy that would have been utilized in competition in a spring is now invested in reproduction.

The spring pool at Saratoga Springs, near the southern edge of Death Valley, contains between 800 and 3,000 pupfish, depending on the time of year (Deacon 1967, 1968). The population is lowest from March to April and reaches its maximum in September. Normally there are about 1,500 fish in the pool. Another large spring, Big Spring in Ash Meadows, Nevada, which contains about 3,000 Amargosa pupfish, also shows annual changes similar to those observed in Saratoga Springs. Largest population numbers occur in spring and early autumn and reduced numbers in winter (Soltz 1974).

Some Amargosa pupfish live in very small constant temperature springs near Devils Hole. These tiny springs (about the size of a wash tub) normally contain between 20 and 150 fish. Mexican Spring, before recently going dry, contained probably the world's smallest, self-sustaining vertebrate population with a population size varying from 20 to 47 individuals (Brown 1971; Soltz 1974). Of these, only four or five were mature males, five to 15 mature females, and the remainder juveniles. Only the constancy of the spring environment and a high reproductive capacity enabled the population to survive in a tiny, long-isolated habitat. Studies of these populations have yielded valuable insights into the life history of pupfish, because it is rare that a scientist can actually count, measure, and observe every individual in a natural population at one time.

The Devils Hole pupfish is probably the most restricted vertebrate species in the world, with *both* the entire population and the entire species naturally existing only in Devils Hole (Wales 1930). Because of its endangered status and unique habitat, much information about population size has been gathered in recent years (James 1968; Deacon and Deacon 1978). Most individuals live in the vicinity of a small rocky shelf or in open water near the surface, but observations by SCUBA divers have shown that some often venture as deep as 26 m into the limestone cavern. At present, the population size fluctuates from a low of about 150–200 fish in winter to 300–400 in summer and early autumn. In the past as many as 800 fish were present during summer, but reduced water levels have decreased the maximum summer population by reducing the critical food supply. Annual changes in population size are known to be related to seasonal food production of algae (Deacon and Deacon 1978).

Fish populations in marshes and streams strikingly contrast with those in spring habitats, in that populations annually oscillate 10 to 20 fold. These estimates are complicated because low winter temperatures cause fish to become inactive and bury in sediments, so that accurate estimates of population size are impossible. Observations strongly suggest stream and marsh populations are seasonally much larger and denser than those in springs. A good example is the Salt Creek pupfish population (Miller 1943). During winter, when the evaporation rate is low, Salt Creek flows for 3 to 6 km along the floor of Death Valley. During spring months,

large numbers of Salt Creek pupfish move into this newly available habitat. A conservative estimate places the population at one million fish during its peak. When summer approaches, the stream begins to dry up at its lower end, isolating large numbers of fish in the remaining pools. By late summer the stream flows for only about 1.0 km below the spring sources and the number of Salt Creek pupfish is reduced to only a few thousand individuals, densely packed in the remaining habitat. Winter floods may further decimate the population.

Populations in marshes formed by the Amargosa River near Tecopa, California, vary less dramatically, but still considerably. During warm months Amargosa pupfish seem to "boil" the water in an attempt to flee from observers. It is not uncommon to capture several hundred fish in a single sweep of a seine net. In winter months the situation is different, with most fish inactive and buried because of the cold water temperature. At this time it is almost impossible to collect a single specimen.

Thermal streams entering marshes provide a special situation. Here the fish are dense and active during the entire year because the source of warm water is constant. In a thermal artesian stream near Tecopa, California, as many as 196 Amargosa pupfish per square meter have been counted, with an average density of about 90/m^2 present throughout the year (Naiman 1976). This is the result of two favorable influences: warm water and an unusually abundant food supply. Fluctuations in population size are still considerable with a 15-fold change observed over the two years this population was monitored.

The Ash Meadows killifish (now extinct) presumably was never very common. Only a few specimens were captured, the last one in 1948. The species frequented the deeper holes of spring pools and was rarely found in spring outflows or marshy areas. Total abundance of this species probably never exceeded a few hundred individuals. Rarity of Ash Meadows killifish presumably reflects strong competition from pupfish and speckled dace. Where competition was lacking, as in nearby Pahrump Valley, killifish were abundant.

The Pahrump killifish, the only native fish in Pahrump Valley, was once abundant in the three large springs in the valley (Miller 1950; Pister 1974). These springs have all been destroyed and only a few survivors remain from the last spring to dry-up, Manse Spring, and are reproducing in two refugia. Consequently, little is known about natural population sizes and densities of Pahrump killifish. Large numbers of killifish were reported from both the constant-temperature spring pools and the variable outflow environments of all three habitats. Presumably these population sizes regularly oscillate, certainly each population reached a density of a few thousand in early autumn. Studies of refuge populations are under way to determine growth rates, maximum population densities, and other life-history information necessary for management of this endangered species.

Little is known about sizes and fluctuations of speckled dace populations because dace are not especially common and are difficult to observe or capture. The largest and densest population inhabits the headwaters of the Amargosa River near Beatty, Nevada. There are no other fish competitors at this locality and the dace population has expanded to utilize all parts of the habitat. In the lower portion of the Amargosa River near Tecopa, California, speckled dace are common, but not very dense. Here they are restricted to cooler riffles and face strong competition from a large Amargosa pupfish population. Speckled dace are even less common and could be considered rare in the larger springs of Ash Meadows, Nevada, where they prefer streams flowing from spring pools. Dace populations in Owens Valley are small and restricted to waters free of introduced predators, such as trout.

Owens suckers are common throughout their range. Although the life history of this species is largely unknown, it numbers in the millions, with particularly large populations in reservoirs on the Owens River. The Owens chub is now restricted to a single population that may reach a summer maximum of about 1,000 fish (Miller 1973). The Mohave chub is restricted to 3 populations at Soda Springs and a number of recently established refuge populations. Many thousands of Mohave chubs exist in all populations combined.

GROWTH RATES

Effects of environmental factors on growth are extremely complex. For example, crowding increases activity of the fish, reduces food intake, and thereby reduces growth rate. Growth is so strongly determined by interacting environmental variables that a general discussion is difficult. However, careful studies of growth have revealed several generalizations.

Juvenile Amargosa pupfish grow faster than adults. Young fish add about 9% new body weight each day, whereas adults increase their weight by only about 1% per day (Naiman 1976). Growth rates similar to these are not unusual for other fishes living in warm environments (such as sunfish, catfish, and largemouth bass). Associated with decreasing growth rate, optimal temperature for growth is highest for juvenile pupfish (about 30°C), shifting downward to between 22–26°C in adults (Kinne and Kinne 1962).

Normally, it takes only 2–4 months for pupfish, dace and killifish to reach maturity after hatching. This length of time varies depending on time of year, water temperature, population density and type of habitat

(spring or marsh). In a marsh, fishes spawned in autumn do not mature until the next spring (about six months), whereas fishes spawned in March or April will be mature by early summer (two months). In constant-temperature warm springs, fishes mature in 2–4 months throughout the year.

Fishes in warm springs grow throughout the entire year at roughly the same rate (Naiman 1976). Growth is slightly depressed over the few winter months, but it is never completely halted. Conversely, fishes in variable temperature marshes and streams do not grow year around. During cold winter months they become dormant (pupfish bury into the substrate) and wait for the warmer spring months. During spring there is a rapid spurt of growth, becoming slightly depressed during the hot summer months and increasing again in autumn when the water cools slightly. The reasons for reduced growth in summer are not sufficiently known, but it could be that large population numbers have reduced the food supply or high water temperatures cause the metabolism of the fish to increase to such a high level that most food eaten is needed for respiration and body maintenance.

SURVIVORSHIP

Survivorship is a concept used to examine how well a group manages to progress through life from birth to death. In other words, once a group of fish hatches, how many live to a certain age or size? Analyses of this type assist ecologists in discovering when during the life cycle is the greatest likelihood of death for an individual in this group. Not surprisingly, this is a major tool originated by life insurance companies for human populations.

The type of survivorship curve depends a great deal upon the environment: whether it is the unpredictable environment of a stream or marsh or the predictable environment of a spring (Fig. 35). In marshes and streams, death is often the result of unpredictable events such as flash floods, desiccating pools, or high temperatures and salinity. These events act on the whole population and are nonselective in the age of individuals they strike. Both old and young fish are destroyed by desiccation of a stream habitat. Generally, in unstable habitats, chances of dying are about the same throughout life once the adolescent stage has been reached.

In spring environments, survivorship takes a different course. Competition between individuals and predation become important, and they are more selective in the age of individuals upon which they act. Events are more predictable and catastrophes such as pools drying up and flash floods are rare occurrences. In all habitats there is high mortality from the egg stage up to about 12 mm (the length at which the fry are strong enough to become free swimming). During this critical period predation by invertebrates takes a heavy toll, as many eggs and fry are eaten by aquatic insects and snails. Once juveniles become strong enough to swim up away from the substrate, the death rate is reduced because they are no longer easily available to predators. Another critical period in spring habitats, especially for male pupfishes, occurs upon maturity. At this time they enter the reproductive population which, for most males, is territorial. Males unable to find or hold a territory are often chased out of the pool by larger and more aggressive males, resulting in death or a shorter life span (Soltz 1974). Some male pupfishes avoid competition by taking on the color pattern of females and show their true color pattern and behavior only when a territory becomes vacant. Once maturity is reached, however, the death rate becomes fairly even without further critical periods until physiological old age.

Speckled dace, chubs, and suckers most likely show survivorship patterns typical of pupfishes in marsh or stream habitats. Dace spawn early in the spring months and will spawn again in late summer if there are sufficient rains to substantially increase stream flow. Undoubtedly there is high mortality from eggs up to the adolescent stage, considering the type of habitat in which they are found and their reproductive strategy of laying large numbers of small (1.0 mm diameter) eggs.

In contrast, killifishes probably have survivorship patterns similar to pupfishes in large spring pools. Killifishes spawn from January to July, live in a stable habitat, and do not lay an especially large number of eggs. Egg development requires about 1–2 weeks. Mortality between egg and adolescent is reduced, and a larger proportion eventually enter the adult population.

LONGEVITY

Average generation time in a population of pupfish, speckled dace, or killifish is only about 2–4 months. This seemingly short time is a result of a number of complex interacting factors including rapid growth to maturity (2–4 months), high reproductive rate, and high mortality rate in young fishes. However, once a fish reaches a strong free swimming stage it may live for 6–9 months. In marshes, where fishes are dormant over the winter, a few individuals may live as long as two or three years.

Longevity depends a great deal on type of habitat. In springs most fishes are relatively short-lived. They are constantly active throughout their life, even in winter, and may only live for 6–9 months after reaching the free swimming stage. In contrast, fishes in marshes and streams often live longer, primarily because they are inactive over winter. It is not uncommon for a fish in these areas to live 12 months or more, and some of the

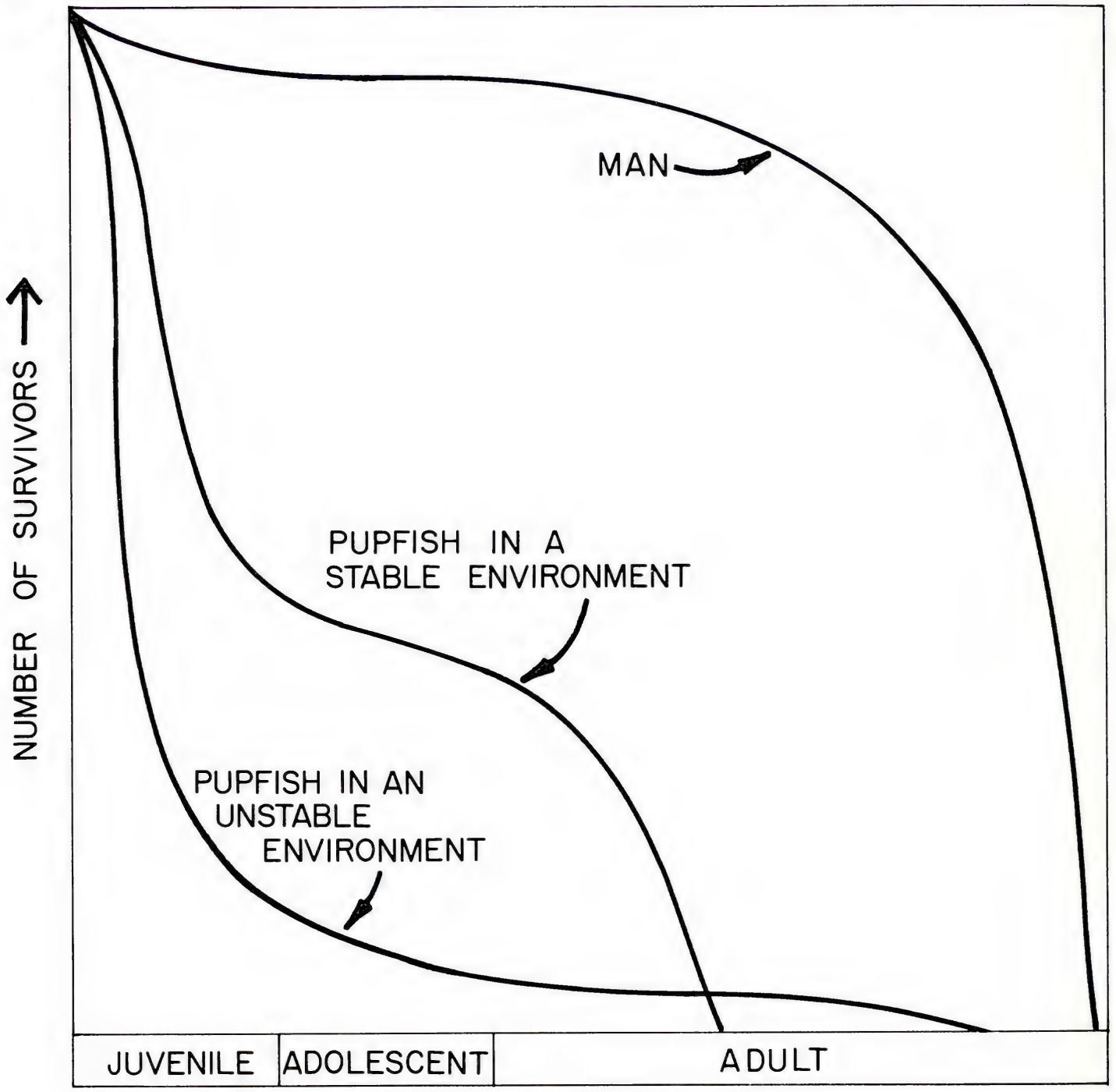

FIGURE 35. Life history and survivorship of pupfish in stable and unstable environments is quite different. There is high mortality in both populations from egg through juvenile stages but it is more evident in pupfish from unstable environments. During adolescence, death rate is fairly even for both populations but changes drastically as adulthood is reached. In spring pools, where competition is keen, death rate increases, whereas in streams and marshes, where competition is lax, death rate remains fairly even with a few individuals becoming very old before death. These survivorship curves contrast sharply with that for humans, where nearly all mortality takes place at an advanced age.

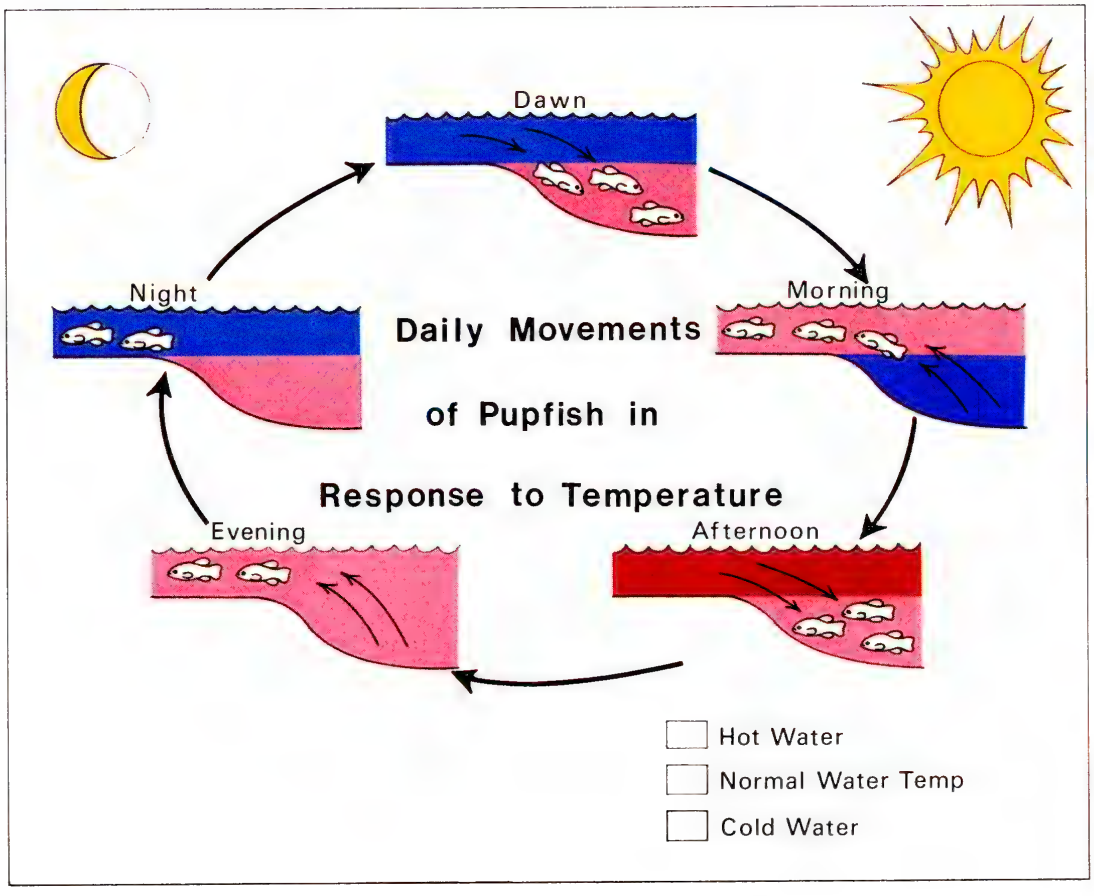

FIGURE 36. Pupfish show consistent daily movements in response to temperature in shallow pools and marshes. Pupfish spend the night in cool shallow water and move into warmer, deeper water at dawn to feed. By mid-morning the shallow water has heated up to a preferred temperature and pupfish return, but by late afternoon this water becomes too warm and they must retreat into deeper water again. During evening this shallow water cools to an optimal temperature allowing the pupfish to return. As darkness encroaches, the fish become less active, resting on the bottom as the water cools, where the remainder of the night is spent.

largest, and presumably oldest specimens have been captured from these types of habitats.

PRODUCTION

Production results from both biomass (weight of fish) and growth rate. Dense fish populations with fast growth rates will have high production rates, whereas sparse populations with normal or slow growth rates have low production. Fish in springs show relatively low rates of production because of low density populations. Marshes and streams, however, with dense populations and relatively rapid growth rates, are highly productive. For example, in a warm stream near Tecopa, California, where there is a dense, fast-growing, Amargosa pupfish population, yearly production is nearly 10 times greater than that of any carnivorous fish population studied to date (Naiman 1976). Although pupfish are not generally thought of as a food fish because of their small size, their potential for food production as fish meal is enormous. A short generation time, omnivorous food habits, adaptability to extreme environments, dense populations, and rapid growth rates all combine to make them extremely productive.

Physiological Ecology

It is important to establish the relationship between an organism and its environment. This presents two major difficulties to ecologists. First, an organism reacts to the total environment rather than to single factors such as temperature, salinity, or dissolved gases. Second, the total environment has to be broken down into single factors, since it is impossible to measure simultaneously all physical, chemical, and biological properties of a natural system. Much of the discussion on temperature, salinity, and dissolved gases is based on studies in which only one environmental variable is monitored. These studies have shown that desert fishes possess many distinct and fascinating adaptations to various environments. Understanding the physiological and biochemical mechanisms responsible for these adaptations provides basic knowledge about functional mechanisms of animal bodies and allows resource managers to make intelligent decisions as stresses of the total environment continue to increase.

Fishes in the Death Valley System live in one of three types of habitat: constant-temperature spring heads; streams and marshes where environmental conditions fluctuate both daily and seasonally; or thermal streams with temperature gradients. Spring habitats provide environments in which temperature, salinity, pH, oxygen, and other physiochemical parameters are nearly constant day after day. In contrast, streams and marshes with fluctuating environments often produce stressful conditions and are characterized as being unpredictable with the possibility of a catastrophe occurring at any time. Summer evaporation nearly dries up many areas, elevating temperature and salinity to near lethal limits. Flash floods may scour the habitat and, in winter, ice may form for considerable periods of time. Thermal streams are unique habitats where hot water arises from the ground and cools as it flows downstream, with the rate of cooling dependent upon local weather conditions. Each of these habitats exert very different selection pressures upon the fish. Rates of evolution, life histories, reproductive strategies, and consequent adaptations to the environment vary in response to habitat type. Not surprisingly, physiological and biochemical adaptations to thermal regimes have been among the most thoroughly studied aspects of desert fishes.

TEMPERATURE

Many records of fishes living at extremely high temperature in nature are doubtful, and it seems likely that any reported observation higher than about 45°C should be questioned and examined carefully (Miller 1949). The maximum constant temperature of water occupied by a reproducing population of fish is rarely greater than 35°C, but some fish can survive exposure to higher temperatures for periods ranging to several hours. A few intensive studies have been conducted in recent years on tolerances, behavior, and biochemical adaptations of both speckled dace and pupfishes to temperature. Killifishes and chubs have not been tested because of their rarity and endangered status.

Temperature Tolerance

Pupfishes are among the most heat-tolerant of all fishes. Upper lethal temperatures (that temperature which can be tolerated for only a short period) commonly range from 40° to 44°C, depending, to some extent, on the recent thermal history of the fish. Pupfish acclimated or living at lower temperatures of 10–20°C can tolerate high temperatures of only 39°–40°C, whereas fish acclimated to temperatures of 25°–35°C can tolerate higher temperatures, up to 42°–44°C (Brown and Feldmeth 1971; Otto and Gerking 1973; Feldmeth, *et al* 1974).

This increased thermal tolerance at higher acclimation temperatures is thought to result from compensatory physiological changes brought about by isoenzymes uniquely suited to function at particular environmental temperatures. Enzymes are molecules that regulate body functions. Isoenzymes are variants of the same basic enzyme molecule, with each variant functioning best over

a narrow range of temperatures. These physiological changes are important to pupfishes as well as to other desert fishes, because summer water temperatures often exceed the maxima tolerated during the winter. Fishes acclimated to cold winter temperatures could not survive a direct transfer to water with a normal summer temperature. The survival value of compensatory physiological adjustment, which allows a progressive seasonal increase in thermal tolerance as the water gradually warms to summer temperatures, is apparent. These compensatory mechanisms enable fish to survive high summer temperatures that would destroy a part or all of the same population in its winter-adjusted physiological state. Such studies on natural populations help biologists understand how other animals may adapt to stresses caused by thermal pollution and provide insight into basic physiological functions.

Tolerance to extreme temperatures changes as pupfishes pass from eggs to juveniles to adults (Shrode 1975; Shrode and Gerking 1977). Eggs show the least tolerance to high temperatures, adults are intermediate, and juveniles withstand the highest temperatures. Amargosa pupfish eggs hatch in a normal manner at temperatures from 20 to 36°C. At higher temperatures the death rate and incidence of deformities rapidly increase. Temperature also affects the length of the incubation period. Between 20 and 30°C incubation requires only 4–5 days and no survival occurs below 12°C. Total body length at hatching is also a function of temperature. The largest fry (5.3 mm) hatch at 24–28°C and the smallest fry (3.6–3.9 mm) at higher temperatures (34–35°C). This is the result of greater respiration at higher temperatures depleting a substantial portion of the egg yolk that would, at lower temperatures, have become body tissue.

The warmest area of the environment is usually shallow water along marsh and stream edges, and this is where the majority of juvenile pupfishes are found. These areas also have the largest daily temperature variations, being cold at night and extremely warm in the afternoon (Naiman, *et al* 1973). Increased resistance of juvenile pupfishes to high temperatures and temperature changes makes them uniquely suited to these areas and may provide them with several advantages, such as escape from predation by larger fishes in shallow water, more available food, and rapid growth (compared to young fish in other habitats).

Adult pupfishes usually stay in deeper, slightly cooler water but at times enter very warm water. Adult fish acclimated to temperatures fluctuating several degrees between afternoon highs and early-morning lows are able to withstand higher temperatures than fish acclimated to constant temperatures, but adults are killed by temperatures 1 to 2°C below those that kill juveniles.

BEHAVIOR

Desert fishes often regulate their body temperature behaviorally by selecting the optimal place in a temperature gradient. In a thermal stream near Tecopa, California, Amargosa pupfish reach their maximum density at temperatures of 32–36°C and move in response to changing temperatures (Brown 1971; Naiman, R.J., unpubl. data). On cold, windy days the water cools quickly below the spring source, and fish move many meters upstream to stay within a comfortable temperature range. Fish move downstream on hot, windless days when the water cools very slowly and optimal temperatures occur far downstream.

In pools on the floor of Death Valley, Cottonball Marsh pupfish move into cool shallow water in early morning and return to constant temperature spring sources in the afternoon as water in the shallows becomes too warm (Naiman, *et al* 1973). Similar observations have been made for the desert pupfish, *Cyprinodon macularius,* in pools along the shore of the Salton Sea, California, and at Quitobaquito Springs, Organ Pipe Cactus National Monument, Arizona (Barlow 1958; Lowe and Heath 1969). In shallow pools, pupfishes show consistent daily patterns of movement that are related to daily changes in temperature regimes (Fig. 36). Pupfish spend nights in the shallowest, coolest areas of pools. At dawn they move into the warmest, deepest areas. Later in the morning, during summer, they work their way into the shallow areas that are beginning to warm. They retreat from shallows when the water temperature exceeds 36–37°C and return when the water cools to the same temperature or below. Moving into more productive warmer water to feed, and then back to cooler water, may lead to maximum use of available food energy by lowering metabolism in cooler water.

DAILY TEMPERATURE CHANGES

Temperatures in shallow marshes and streams may fluctuate as much as 15–20°C in one day (Naiman, *et al* 1973; Naiman 1976). During midsummer, at Cottonball Marsh, temperature ranges of 15°C have been measured. Changes of this magnitude, or greater, also occur in the lower reaches of Salt Creek, along the Amargosa River, in the marsh at Saratoga Springs, and probably at several other locations. This is of considerable ecological importance because few fishes other than pupfishes are able to withstand such wide daily oscillations (Fig. 37). Most fish species never experience temperature changes of more than a few degrees in a single day. In laboratory experiments, fluctuating temperatures of 20°C increase the temperature range at which pupfishes remain active (Feldmeth, *et al* 1974).

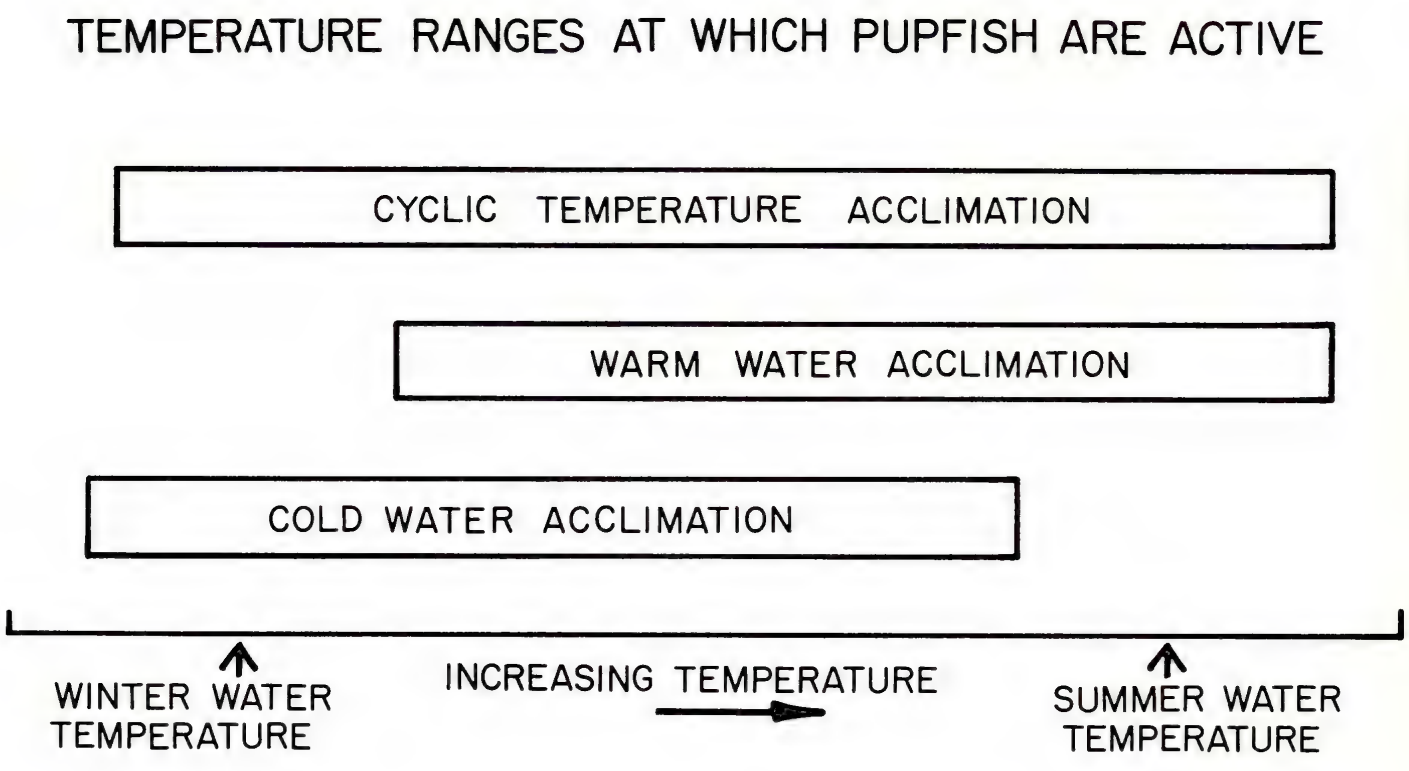

FIGURE 37. The range of temperatures at which pupfish are active depends on their recent thermal history. The absolute range of temperatures tolerated does not change in response to cold or warm acclimation but rather shifts up and down the temperature scale. For example, if cold acclimated pupfish are gradually exposed to warmer water the temperature range tolerated will gradually shift toward higher temperatures. Cyclic temperature acclimation, however, will increase the total range tolerated by pupfish, and both high and low temperature tolerances will be increased.

That is, their tolerance to both high and low temperatures is increased (probably as a result of the induction of temperature-specific isoenzymes). Research on this aspect of fish ecology is just beginning and promises to yield valuable information on biochemical adaptations of fish to their environment.

In thermal streams, fish may live in water only 1 or 2°C below their upper incipient, lethal temperature (that temperature which may be tolerated indefinitely) and will feed in areas only 1 or 2°C below their critical thermal maximum (the temperature that can be tolerated for only a few seconds). Figure 38 illustrates the situation at Tecopa Bore, a thermal artesian stream near Tecopa, California. Amargosa pupfish follow the 42°C isotherm along stream edges, when, only centimeters away, the temperature in the center of the stream is above their critical thermal maximum (Brown 1971). As observers walk along the bank, an occasional pupfish will dart into the stream center and die immediately because the water is too hot to be tolerated for even a few seconds.

Temperature studies on speckled dace are few in contrast to those on pupfishes. Dace often inhabit the same waters as pupfish but are more commonly found in cooler riffles. The upper incipient lethal temperature for young fish is about 33°C and for adults it is 32°C (John 1964). In addition, older fish die after less exposure to increasing temperature. Adult dace often die while juveniles may survive in evaporating pools, cut off from the main stream. This fact is of considerable potential importance, in that a few young fish may survive a catastrophe and perpetuate the population.

SALINITY

Desert waters are not only characterized by thermal extremes but also by greatly varying salinities. This is a natural consequence of surface water standing in a warm, dry environment. The evaporation rate is very high, and flushing action which maintains the fresh character of water in areas with more rainfall is an infrequent occurrence in deserts. It is not surprising that some of the most striking adaptations to hypersaline conditions are found among desert fishes and their relatives.

Salinity is an important environmental variable because it affects water and ionic balances within fishes. For example, fishes living in fresh water gain water without drinking because the higher ion concentration in their body causes water to flow into their tissues through a process called osmosis (Fig. 39). In contrast, fishes living in sea water tend to lose water because the surrounding medium (35 parts per thousand [‰] salinity) is more saline than the fish's body fluids (15‰ salinity). These fishes are faced with the problem of dehydration, must actively drink saline water, and remove the salts by excreting them from the kidneys and gills to maintain a normal salt balance. Desert fishes occasionally are faced with near-lethal, osmotic stress as salinities rise to far above that of sea water. Studies of how these fish respond to this stress reveal some interesting and unique physiological mechanisms enabling them to prosper in these unusual habitats.

Fishes from several different evolutionary groups have the capability of persisting in salinities up to two or three times the concentration of sea water, and a few reports imply survival at considerably greater concentrations (Deacon and Minckley 1974). Pupfishes belong to one of these groups and their capabilities are readily demonstrated in several Death Valley species. The Cottonball Marsh pupfish has been found to withstand salinities 2.5 times that of sea water — 88‰, (Naiman, *et al* 1976). With gradual acclimation, a few individuals withstood 130‰ (3.7 times sea water) for several weeks and were in good health when the experiments ended. Hunt, *et al* (1966) report this pupfish living at 160‰ in a natural situation but in our field studies fish did not voluntarily frequent water above 70‰. Most fish preferred salinities between 22 and 45‰.

Other pupfish also tolerate high salinities. Desert pupfish, like the Cottonball Marsh pupfish, can withstand salinities 2.5 times that of sea water (Barlow 1958), and a close relative of these species, living along the Texas coast, has been found in water four times more saline than sea water (Simpson and Gunter 1956). Most pupfishes easily withstand salinities of at least twice sea water, as many species inhabit marshes and streams where partial drying of habitat is frequent. Selection pressure for tolerance to high salinities is strong in these habitats, and it is not surprising that pupfishes have evolved mechanisms for dealing with these situations.

Tolerances to extremely low salinities in desert fishes have been studied less. Pupfishes will easily survive in normal fresh water but it is remarkable that the Salt Creek and Cottonball Marsh pupfish have been maintained in near distilled water (water lacking dissolved ions). Likewise, eggs of desert pupfish will develop in distilled water although mortality is high (LaBounty, J., pers. comm.). This demonstrates a remarkable ability to regulate the water and ionic content of their bodies, a feat far beyond the capability of most fishes.

Salinity tolerance during different stages of the life cycle varies in a manner similar to temperature tolerances. Observations of pupfish in drying pools indicate juveniles have a greater salt tolerance than do eggs, fry, or adults. For example, eggs of desert pupfish fail to develop above 70‰, adults die at about 85‰, and juveniles survive to about 90‰ salinity (Kinne and Kinne 1962).

FIGURE 38. Fish in thermal streams distribute themselves in response to the temperature gradient. Although pupfish cannot live indefinitely at high temperatures, they will spend various periods of time at temperatures up to 42°C. As the temperature regime moves up or down stream in response to local weather conditions, the fish will also move but never enter water above 42°C. Sometimes groups of fish will be trapped in small, cooler side pools along the stream edge where they wait for mainstream water to cool before again reentering the main population.

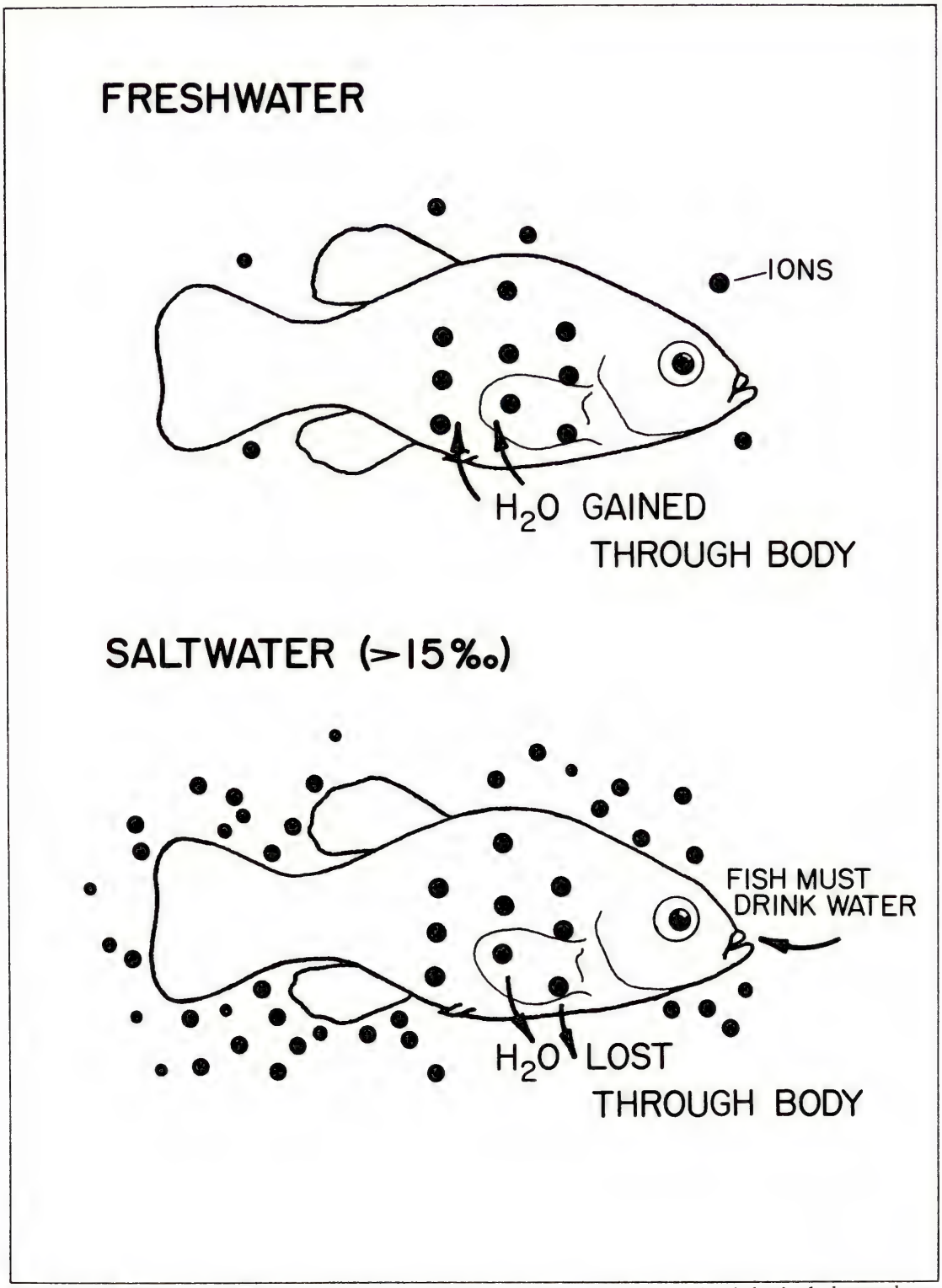

FIGURE 39. Many desert fishes live in hypersaline waters in which physiological demands on their bodies are quite different as compared to fishes in fresh water. Freshwater fishes gain water through their body without drinking because the concentration of ions in their body far exceeds that of the surrounding water. In contrast, fishes in salt water (>15 ‰) are faced with the problem of dehydration because the concentration of ions in the environment far exceeds that in their bodies causing water to be drained out. Fishes in this situation must drink the salty water, remove the excess ions internally and excrete them via the kidneys or gills. The saltier the water the more stressful it becomes to physiological mechanisms controlling body homeostasis.

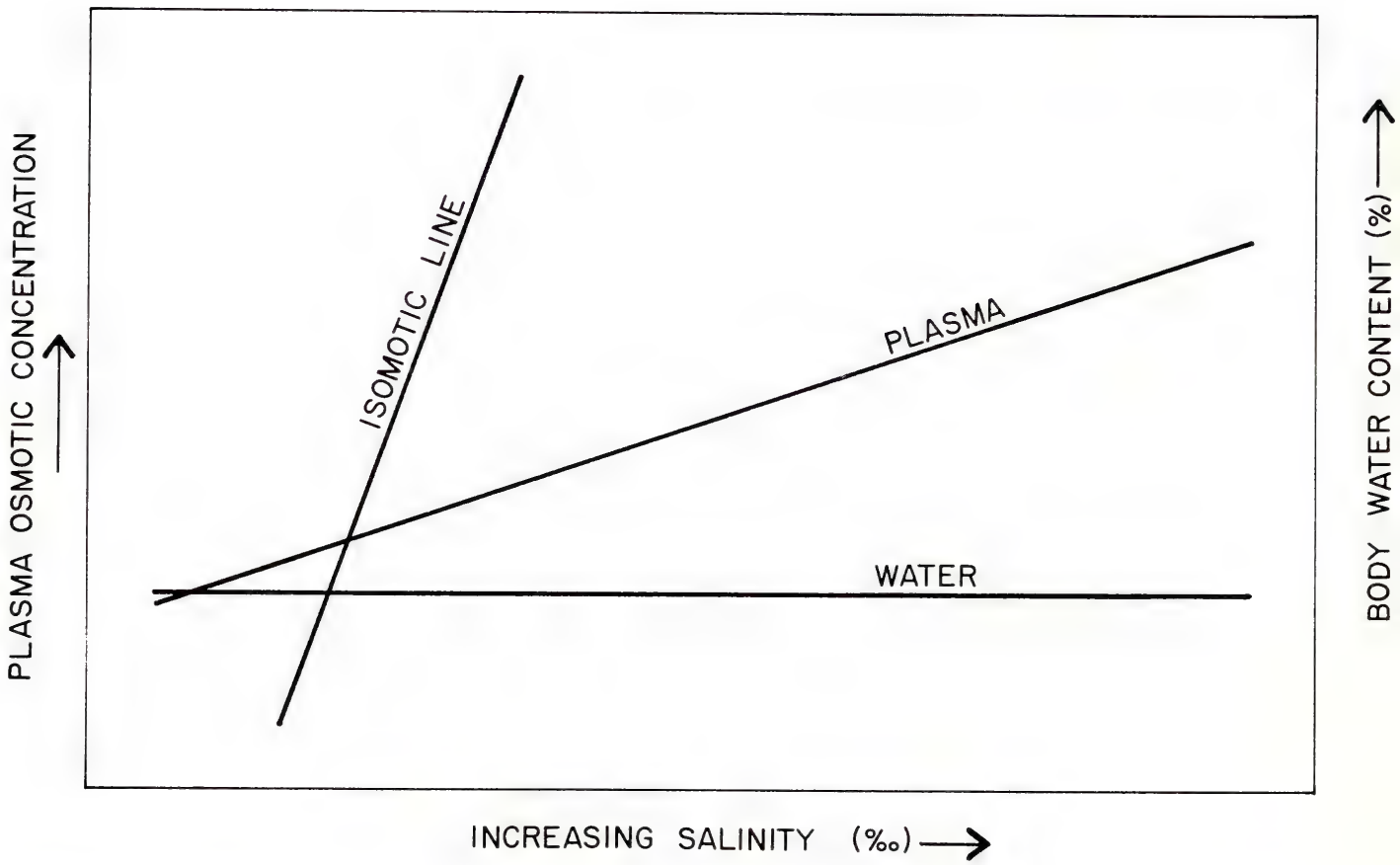

FIGURE 40. Pupfishes in hypersaline water have interesting physiological responses to this stressful situation. The percentage of body water remains nearly constant up to time of death, implying they do not dehydrate in saline water. The osmotic concentration of blood serum slightly increases in order to reduce the difference in ionic concentration between their body and the environment, but it does not increase in absolute terms as shown by the isosmotic line.

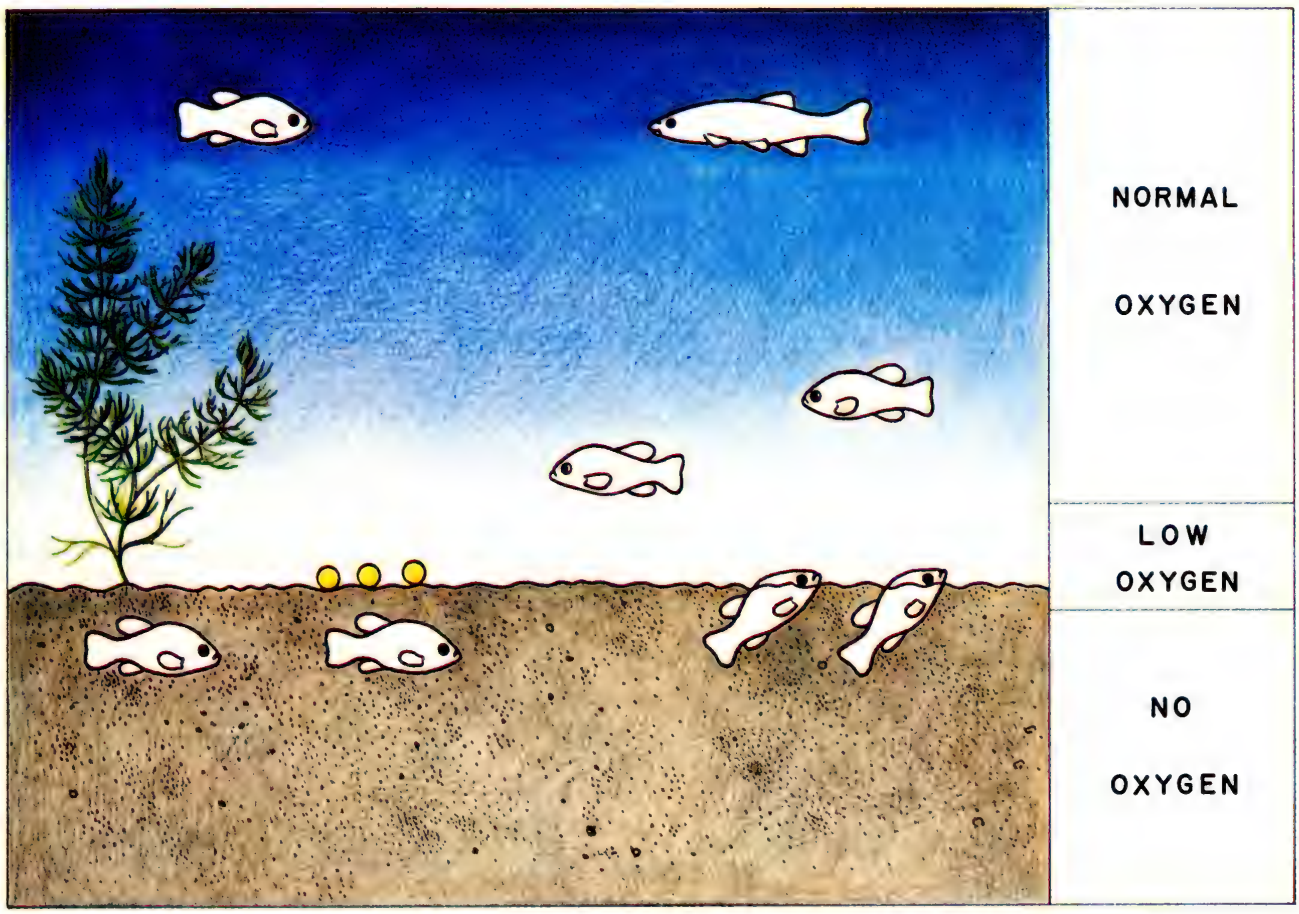

FIGURE 41. Amount of oxygen in an aquatic ecosystem is not uniform. Normal oxygen concentrations occur in the water column where all desert fishes can survive. Low oxygen concentrations can occur at the mud-water interface and be stressful or near-lethal to eggs and fish found in this area. Some pupfishes are known to bury into the oxygen-deficient sediments but how they survive there is not known.

The ability of desert fishes to tolerate wide salinities seems based upon specialized physiological and biochemical mechanisms. Nearly all fishes investigated show an initial tendency to desiccate when exposed to hypersaline waters. Pupfishes are unique because they are able to recover from this stress very quickly (in about eight hours) and readjust their blood physiology to suit the new conditions (Renfro and Hill 1971). In other fishes which move between salt and fresh water (such as steelhead trout and eels) this readjustment takes between 50 and 170 hours.

Pupfishes adjust their blood serum concentration in response to the salinity (Fig. 40). As salinity increases, osmotic concentration of their serum increases slightly, helping to minimize stress incurred by living in hypersaline waters by reducing the difference in ionic concentrations between the fish's body and the surrounding water. This unusual mechanism is apparently accomplished without loss of water (Naiman, *et al* 1976). The percentage of water in the body remains nearly constant throughout the range of salinities tolerated. In general, pupfishes are considered extremely tolerant of a wide range of saline conditions.

Salinity tolerance of speckled dace, chubs, Owens suckers, and killifishes has never been investigated. Observations on the types of habitats frequented by these fishes suggests none are exceptional in this regard. Dace, chubs, and suckers do not occur in areas where partial drying of habitat is common or in normally saline habitats. They are found only in fast portions of streams or in large springs where salt concentrations are rarely, if ever, severe. Killifishes are restricted to large springs with a constant environment but have evolved from a group of fishes which includes many salt-tolerant species. Killifishes may be somewhat salt tolerant but this ability, if present, has probably not been utilized for many thousand of years.

DISSOLVED GASES

Oxygen, carbon dioxide, and hydrogen sulfide are important environmental factors in desert waters. Investigation of their effects on pupfishes, killifishes, and speckled dace has just started. Oxygen and carbon dioxide are considered to be limiting environmental factors, the effect of which at stressful concentrations is to restrict or decrease activity. A decrease in oxygen or an increase in carbon dioxide operate in the same way by restricting the supply of oxygen to the tissues. In contrast, hydrogen sulfide at high concentrations is considered a lethal environmental factor because of its toxicity.

Oxygen

Tolerances to low oxygen concentrations are known for a few desert fishes. The lowest minimum for all fishes, 0.13–0.22 mg oxygen/liter, is for desert pupfish (Lowe, *et al* 1967). Normally, water contains 50 to 70 times this concentration. Other species of pupfish can probably survive similar concentrations. For example, Amargosa pupfish are known to dive into the oxygen deficient mud bottoms of their habitats, where they frequently bury themselves completely, but will sometimes keep their mouth or entire head exposed to obtain oxygen from the water (Fig. 41). Individuals have been found 2 cm below the mud-water interface and certainly could not obtain oxygen from above the mud surface. Some pupfish species may have the ability to survive for long periods during winter under anaerobic conditions (without oxygen), but this feature of their physiology is not yet fully understood.

Daily changes in oxygen content of water in large springs rarely involve decreases below critical levels. However, in small pools or shallow marshes, wide fluctuations are common (Hubbs, *et al* 1967). Very low oxygen concentrations occur at the mud-water interface and possibly beneath beds of aquatic plants. Pupfish eggs deposited on bottom sediments in these habitats must be capable of resisting considerable periods of low oxygen. Low oxygen concentrations have been shown to retard embryonic development. Observations suggest that developmental retardation is more pronounced in stagnant, low oxygen water than in moving water at the same oxygen level, because water movement allows a more efficient exchange of respiratory gases at the egg surface. Extreme conditions of oxygen (or temperature and salinity) can temporarily stop embryonic development (Deacon and Minckley 1974). Development will proceed in a normal manner if conditions are normalized within hours or a few days; longer periods cause irreversible damage and are lethal. This indicates the adverse conditions to which eggs are often exposed at the mud-water interface may not necessarily be entirely detrimental, provided favorable conditions prevail for a portion of each day.

Carbon Dioxide

Desert habitats rarely contain concentrations of free carbon dioxide sufficiently high to create problems for fishes. Highest concentrations are usually in springs where, in most instances, large quantities of dissolved solids tend to buffer any direct effects of the gas. No desert fishes have been specifically studied with respect to their tolerance of carbon dioxide, but casual observa-

tions suggest that pupfishes can tolerate high concentrations.

HYDROGEN SULFIDE

Hydrogen sulfide is commonly present within the mud bottoms of desert aquatic habitats, but very few measurements of its concentration are available. When hydrogen sulfide is present, little or no oxygen is available. Bottom muds seem to have relatively high concentrations of hydrogen sulfide, on the basis of the characteristic smell of rotten eggs of many habitats when disturbed. The toxicity of hydrogen sulfide is caused by sulfide, which creates a tissue anoxia resulting from inactivation of respiratory carriers. If concentrations are not too great, sulfide may be oxidized within the body to relatively harmless sulfate. Pupfishes often spend long periods of time, especially in winter, within such sediments. Toxicity at these times would presumably be near lethal, but it seems probable that pupfishes and their relatives may have evolved physiological means of coping with hydrogen sulfide.

Practically nothing is known about tolerances of killifishes to dissolved gases. However, since many of their relatives are tolerant to environmental extremes, it would not be surprising to find that killifishes have also developed adaptations to dissolved gases.

OTHER SPECIES

Speckled dace, chubs, and suckers are very intolerant to abnormal gas concentrations. Dace begin to die rapidly when the oxygen concentration drops below 2.0 mg/l; survivors exist only by gulping air from the water surface (John 1964). Their habitats are generally characterized as having normal oxygen and carbon dioxide concentrations and very little hydrogen sulfide. For this reason, natural selection appears not to have caused dace, chubs, or suckers to develop mechanisms similar to those presumably evolved by pupfishes for existing in waters where dissolved gases can be stressful.

FIGURE 42. Water being mined from the underground aquifer supplying the springs in Ash Meadows, Nevada. James Yoakum.

CONSERVATION OF DESERT FISHES

To fish in troubled waters.
Matthew Henry. *Commentaries. Psalm IX.*

Fishes are just one group of the community complex in springs, marshes and streams of the Death Valley System. It is emotionally easy, but ecologically irresponsible, to preserve fish while ignoring endemic snails, aquatic insects, and other invertebrates and plants. Disruption at any level of the ecosystem has unstabilizing repercussions throughout the entire system. When this occurs selection pressures change and the possibility of extinction increases. Obviously the fish are totally dependent upon the integrity of the fragile, isolated ecosystems in which they evolved. The necessity of maintaining intact desert aquatic ecosystems should be the underlying philosophy behind any conservation program.

Water is the critical limiting resource for most life in Death Valley and all desert areas. Consequently, the influence of surface water in Death Valley extends far beyond the confines of aquatic habitats. Desert shrubs and wildflowers abound in the vicinity of water and provide habitat and food for wildlife concentrated nearby. Large, wide-ranging mammals such as coyote and bighorn sheep also frequent many springs and streams. Reduction and loss of water in the Death Valley System is much more than a threat to the fishes; it seriously endangers the entire desert ecosystem.

Desert fishes are the first vertebrates to be affected by alteration and disruption of limited surface water. Over the past 35 years, man's disruptions in the Death Valley area have resulted in extinction of one fish species (Ash Meadows killifish) and three or four of the 11 recognized subspecies (Raycraft Ranch killifish, Pahrump Ranch killifish, Shoshone pupfish and Tecopa pupfish). Another species (Owens pupfish) and two subspecies of minnow (Owens chub and Mohave chub) that were once abundant and wide ranging are now each restricted to a single habitat in their native range. The Manse Ranch killifish, the only remaining member of the genus *Empetrichthys,* survives only in refugia outside its native Pahrump Valley. None of the 18 native fishes of the Death Valley System have been unaffected by man, and, at most, only five can be considered healthy and undepleted (Table 2).

There are four main causes for the decline and extinction of desert fishes. One is introduction of exotic, non-native (often predatory) fishes and other organisms into their habitats. Second is direct poisoning by or accumulation of pesticides in aquatic ecosystems. Third is disturbance of habitats via diversion of surface water. Fourth, and most serious, is mining of groundwater. The fact that many fish habitats in the Death Valley System have been subjected simultaneously to two or three of these disruptions greatly increases the chance of potentially disastrous consequences.

Introduction of exotic species into isolated, relatively simple ecosystems has been highly disruptive because exotics are potential competitors or predators of native fishes (Miller 1961). Many desert fish populations have evolved in nearly complete absence of either predators or competitors. In addition, introduction of a closely related species may result in loss of native species through hybridization as the unique gene pool is modified or destroyed.

Mosquitofish *(Gambusia affinis),* introduced throughout the western United States for mosquito control, have depleted many native fish populations through predation and competition for food and space (Minckley 1973). Pupfishes have been shown to be more effective at eating mosquito larvae, yet mosquitofish have been introduced into most pupfish habitats. Once established, mosquitofish compete with pupfish for limited invertebrate food items, displace pupfish from portions of the habitat, and prey on pupfish eggs and fry.

Some springs in Ash Meadows have suffered the effects of illegally introduced exotic species. Mosquitofish, mollies, platyfish, bullfrogs, crayfish and largemouth bass have been found in several of the larger

TABLE 2. Present status of the fishes of the Death Valley drainage system.*

	STATUS			
	Stable	Threatened	Endangered	Extinct
Pupfish – Cyprinodontidae				
Owens pupfish *(Cyprinodon radiosus)*			X	
Salt Creek pupfish *(Cyprinodon salinus)*	X			
Cottonball Marsh pupfish *(Cyprinodon milleri)*	X			
Saratoga Springs pupfish *(Cyprinodon nevadensis nevadensis)*	X			
Amargosa River pupfish *(Cyprinodon n. amargosae)*	X			
Tecopa pupfish *(Cyprinodon n. calidae)*				X
Shoshone pupfish *(Cyprinodon n. shoshone)*				X
Ash Meadows pupfish *(Cyprinodon n. mionectes)*	X			
Warm Springs pupfish *(Cyprinodon n. pectoralis)*			X	
Devils Hole pupfish *(Cyprinodon diabolis)*			X	
Manse Ranch killifish *(Empetrichthys latos latos)*			X	
Pahrump Ranch killifish *(Empetrichthys l. pahrump)*				X
Raycraft Ranch killifish *(Empetrichthys l. concavus)*				X
Ash Meadow killifish *(Empetrichthys merriami)*				X
Minnows – Cyprinidae				
Owens chub *(Gila bicolor snyderi)*		X		
Mohave chub *(Gila bicolor mohavensis)*			X	
Speckled dace *(Rhinichthys osculus)*	X			
Suckers – Catostomidae				
Owens sucker *(Catostomus fumeiventris)*	X			

* as listed by U.S. Dept. of Interior

springs. This situation was aggravated by the illegal operation of a tropical fish farm at Forest Spring in the early 1960's, which resulted in the temporary residence of such exotics as the arawana *(Osteoglossum bicirrhosum)*, a large South American fish predator. Establishment of three or four exotics in most of the large springs in Ash Meadows apparently resulted in extinction of the rare Ash Meadows killifish over 25 years ago. Today, populations of Ash Meadows pupfish in these same springs are depleted due to competition with exotic species. In Big Spring, territorial male pupfish devote most of their time and energy to chasing intruding mollies, mosquitofish, bullfrogs, tadpoles or crayfish instead of spawning.

A voracious fish predator, largemouth bass *(Micropterus salmoides)*, rapidly exterminated all native fishes (Ash Meadows pupfish, killifish and speckled dace) in Crystal Pool. This species and other game fish, primarily trout, introduced into the Owens River drainage nearly eliminated the Owens pupfish and depleted the populations of three other native fishes. Fortunately, largemouth bass did not become widespread in the Amargosa River drainage and apparently have been eliminated.

Both the Owens and Mohave chub subspecies have hybridized with chubs introduced from other areas. Hybridization results in the mixing of gene pools of the two parent species to form an intermediate type, the hybrid. In these two cases, hybridization has been so extensive that the native parent-type can no longer be identified. Only a single genetically pure population of each subspecies exists today: the Owens chub in the old river channel in Owens Gorge and the Mohave chub in Soda Springs. Likewise, pupfishes readily hybridize in the laboratory. No natural hybrids of Death Valley pupfish have been identified but the Amargosa River pupfish may have hybridized with, and genetically swamped any remaining Tecopa pupfish when their habitats were connected by channelization of spring outlets at Tecopa Hot Springs. The potential danger of irresponsible transport of pupfish between habitats is enormous, obvious, and a violation of the law in California.

Although pesticide poisonings of desert fish populations have not been definitely documented, the hazard is real. Fishes accumulate DDT and related pesticides in their bodies until lethal concentrations are reached. Cases of fish poisoning and mass deaths due to mis-

handling of pesticide applications are not uncommon in agricultural areas of the United States. Proliferation of agricultural developments in the Death Valley System increases danger of fish poisoning from pesticides entering small aquatic habitats. Pesticide poisoning is suspected to have been partially responsible for extermination of the Shoshone pupfish.

Severe habitat alteration resulting from diversion of spring flows and appropriation of surface water has become the major threat to desert fishes. The most extreme case is the alteration of stream systems in Owens Valley and export of Owens River water by the City of Los Angeles. Dams were constructed to impound water and reduce flooding, while the lower river was channelized or diverted for much of its course. These modifications drastically reduced the marshy habitat of Owens pupfish and greatly diminished the optimal habitat for the speckled dace, suckers and chubs. The Owens pupfish population rapidly declined from millions in 1916 to a few hundred individuals by the 1930's. The species was thought to be extinct when described in 1948. Owens pupfish were rediscovered in 1956 in Fish Slough, a relatively undisturbed marsh north of Bishop. They were not seen again until 1964, and in 1969 their last remaining habitat dried up. The species was saved by California Department of Fish and Game personnel literally hand-carrying about 200 survivors to a permanent spring in another area of Fish Slough (Miller and Pister 1971).

In Ash Meadows, a number of the larger spring outflows coalesced to form an extensive marsh known as Carson Slough. This habitat supported thousands of Ash Meadows pupfish and speckled dace. Carson Slough was drained in the early 1960's to facilitate peat mining. Total destruction of this habitat seriously depleted two of the four native fishes in Ash Meadows.

Spring outflows are commonly channelized and streamside vegetation removed to increase water availability downstream for consumptive uses. Such drastic habitat alteration seriously disrupts spring ecosystems. Often, outflow habitat is more productive than the spring pool, thus supporting a majority of the fish population. Tecopa pupfish were exterminated from their type locality, Tecopa Hot Springs, when the outflow stream was channelized to increase flow rate. The most blatant example of habitat destruction was the blasting and bulldozing of Raycraft Springs to divert the flow to other areas of Pahrump Valley in 1955. The result was the immediate and total extermination of one of the three subspecies of Pahrump killifish.

The ''need'' for more and more water for development of agriculture in desert areas has resulted in pumping water from underground aquifers (Fig. 42). This relatively recent practice poses by far the most serious threat to fishes in the Death Valley System, particularly those in the Amargosa River drainage. In this area pumping is actually mining the water table (Dudley and Larson 1976). This occurs when pumpage exceeds recharge of underground aquifers, resulting in inevitable lowering of spring flows. In Pahrump Valley, groundwater has been mined at the tremendous average annual rate of 3,200 hectare-meters per year for over 20 years. As a result, all major springs in the valley are dry and the native fish, the Pahrump killifish, has been eliminated.

Major agricultural development in Ash Meadows since 1969 has resulted in a rapid reduction of spring flows and destruction of fish habitat (Deacon and Bunnell 1970). Point of Rocks Spring, one of the most beautiful in the area, has been ravaged (Fig. 43a, b). Its water now flows through two headgates and a 100-horsepower pump is located immediately adjacent to the spring. Miraculously, a small population of pupfish still survives. the pupfish and speckled dace in Jackrabbit Spring, however, were completely eliminated when a pump suspended directly over the springhead drained the habitat completely dry (Fig. 44a, b). Flow from all springs in Ash Meadows has decreased to varying extents since heavy pumping commenced in 1970.

Devils Hole is the only natural habitat of the endangered Devils Hole pupfish, a unique species and most remarkable of all pupfish in the Death Valley System (Fig. 45). Water level in Devils Hole, which has no surface outlet, is directly determined by the amount of water in the vast underground aquifer. Consequently, mining of groundwater in Ash Meadows directly lowers the water level in Devils Hole and progressively exposes the shallow limestone shelf upon which the small pupfish population depends for food and spawning area (Fig. 46).

Stabilization of the water level in Devils Hole approximately one meter below a fixed reference point is the result of recent legal action to regulate pumping. The one-meter level has been shown to cover enough of the shelf habitat to maintain a stable pupfish population, although it now averages about half of its former maximum number of 800 individuals (Deacon and Deacon 1978). The suit was filed in Federal Court by the U. S. Justice Department for the National Park Service, culminating in a U. S. Supreme Court decision in Cappert vs. United States handed down in June, 1976 (Sanchez 1976). This decision has significance far beyond the particular plight of the Devils Hole pupfish. For the first time, the high court asserted the right of the federal government to appropriate groundwater for the preservation of natural aquatic ecosystems.

Increased awareness of rapid deterioration of aquatic habitats in the Death Valley System and the immediate threat of extinction for many endemic fishes prompted a meeting in November 1969 of scientists representing several universities, state and federal resource man-

FIGURE 43a. Point-of-Rocks Spring, Ash Meadows, Nevada, circa 1966. Robert Liu.
43b. Point-of-Rocks Spring after the removal of vegetation and stream channelization, April 1969. E.P. Pister.

agement agencies, and private conservationists. At this symposium, held at Death Valley National Monument, the plight of the Death Valley System fishes, several of which were already listed as endangered species, was discussed. Basic plans for species preservation and habitat conservation were developed. Various individuals and agencies left with assigned tasks to perform, and most were critically important in pulling these fish back from the brink of extinction.

In May 1970, a "Pupfish Task Force" was established by the Secretary of the Interior to coordinate the preservation program. A second symposium was held at Death Valley National Monument in November 1970. Progress of the various preservation programs and status of endangered species were reviewed and updated. The most significant accomplishment of this meeting was the establishment of the Desert Fishes Council, whose purpose is ". . . to provide for the exchange and transmittal of information on the status, protection and management of the desert fishes and their habitats." The original membership of the Council included representatives of California and Nevada Fish and Game Departments, National Park Service, Bureau of Sport Fisheries and Wildlife, Bureau of Land Management, U. S. Geological Survey, Universities of California, Michigan, and Nevada, various conservation organizations and concerned private individuals. Those in attendance left with a unified set of goals, sense of purpose and guarded optimism about possible preservation of Death Valley System fishes.

The Desert Fishes Council has continued to play the primary role in coordinating preservation efforts. These efforts include basic research on the biology and habitat requirements of the fishes, water use surveillance, hydrologic studies, location and development of transplant sites and refugia, aquarium culture, land reclassification, legal action, legislative action, and publicity.

Knowledge of how to manage desert fish habitats has advanced tremendously in the past nine years. Extensive hydrologic studies of the Amargosa River drainage indicate the total dependence of springs in Ash Meadows on major interbasin movement of groundwater. As the Devils Hole case has shown, pumping can have an immediate detrimental effect on spring flows. The concept of critical habitat takes into account extent and integrity of entire aquatic ecosystems, not just the habitat of a particular fish. Research into population biology and physiological ecology of various fish species aids management programs. Studies of the interaction between terrestrial and aquatic components of desert ecosystems aid habitat managers in maintaining long-term integrity of entire ecosystems, which is essential for permanent preservation of desert fishes under natural conditions. At the time of this writing, scientists have accumulated sufficient experience and basic knowledge of Death Valley System fishes and their habitats to formulate and carry out comprehensive long-term management programs.

Transplanting of fishes to refugia from populations seemingly on the brink of extinction has been necessary in the past. For example, pupfish from Devils Hole have been transferred into five, apparently suitable, spring habitats widely scattered over the deserts of California and Nevada. None of these transplants established reproducing populations. An artificial refugium constructed below Hoover Dam, however, now contains a reproducing population of Devils Hole pupfish, but the fish are larger, of unusual proportions, and the rate of reproduction has drastically declined, yet the population has maintained itself for over five years (Williams 1977).

The most dramatic example is that of the Pahrump killifish, which survives only in refugia. Relatively large reproducing populations of Pahrump killifish have been established in ponds at Corn Creek, near Las Vegas, and in an isolated canyon above the Colorado River. A third population was established in an artificial refugium in Ash Meadows, but it died out in 1977. As with the Devils Hole pupfish, individuals in all refugium populations are larger and somewhat morphologically different from the parent population.

When the habitat of a species changes, as in these refugia, selection pressure on the fishes changes, resulting in gradual evolution of a type better adapted to the new habitat. Thus, the gene pool is altered, and the original species is gone. Therefore, transplanting of fishes is only done when the last natural habitat has deteriorated to a point where species face certain extinction. Transplanted fish, if they become established in a refugium, are not truly representative of the endemic species. This problem applies equally to aquarium bred fishes and to other vertebrates, even such well known species as the bison. This approach should only be used for one or two generations to build stocks for reintroduction into native habitats. Unfortunately, the two most endangered species, Devils Hole pupfish and Pahrump killifish, have not been successfully reared despite attempts by highly qualified aquarists.

In areas of Death Valley System where water is still ample and native fishes are threatened primarily by introduced exotic species, refugia in native waters are highly desirable. The Owens Valley Native Fish Sanctuary in Fish Slough is a highly successful refugium of this type (Fig. 47). It now contains large populations of Owens pupfish and has been stocked with small numbers of Owens chub, Owens suckers, and Owens speckled dace. Only here and in two smaller refugia are the native fishes of Owens Valley protected from the many introduced exotic species.

Numerous attempts have been made to conserve portions of fish habitats by purchase or legislation. The

Nature Conservancy has purchased Big Springs in Ash Meadows, Nevada, and the surrounding 33 hectares. A bill introduced in the U. S. Senate in early 1978 would create a Desert Pupfish National Wildlife Refuge covering all of Ash Meadows. Amargosa Canyon has been given protected status by the Bureau of Land Management. Soda Springs, last habitat of the Mohave chub, is now protected by the Bureau of Land Management and the California State Universities and Colleges. The Owens Valley Native Fish Sanctuary in Fish Slough has been set aside as an ecological reserve by the State of California, and the entirety of the Slough is being considered for management as a natural area under interagency administration involving the California Department of Fish and Game, Bureau of Land Management, City of Los Angeles, and University of California. A portion will comprise a unit of the University's Natural Land and Water Reserves System.

The effort to conserve the fishes of the Death Valley System and their unique habitats is active, strong, and well directed. Much has been learned about desert fish biology, aquatic ecosystems, hydrology, and management of desert fishes and their unique habitats. Thus, we are in a position to successfully preserve and maintain desert ecosystems, their endemic fishes, and other forms of life. If this is to be successful it will take a *permanent* philosophical and financial commitment from all involved. However, in light of recent deterioration of Death Valley aquatic ecosystems and ever increasing demand for water by the rapidly growing population of the arid southwestern United States, many springs may be threatened if not destroyed in the next 20 years, even those in Death Valley National Monument. Some aquatic habitats and fishes in the Death Valley System must be preserved because they reflect the quality of the environment and can never be regenerated once they are radically altered or destroyed. The choices are obvious and the knowledge and tools are at hand to achieve a compromise. We must all make the decision, and it must be made soon, or there will be no native fishes of Death Valley.

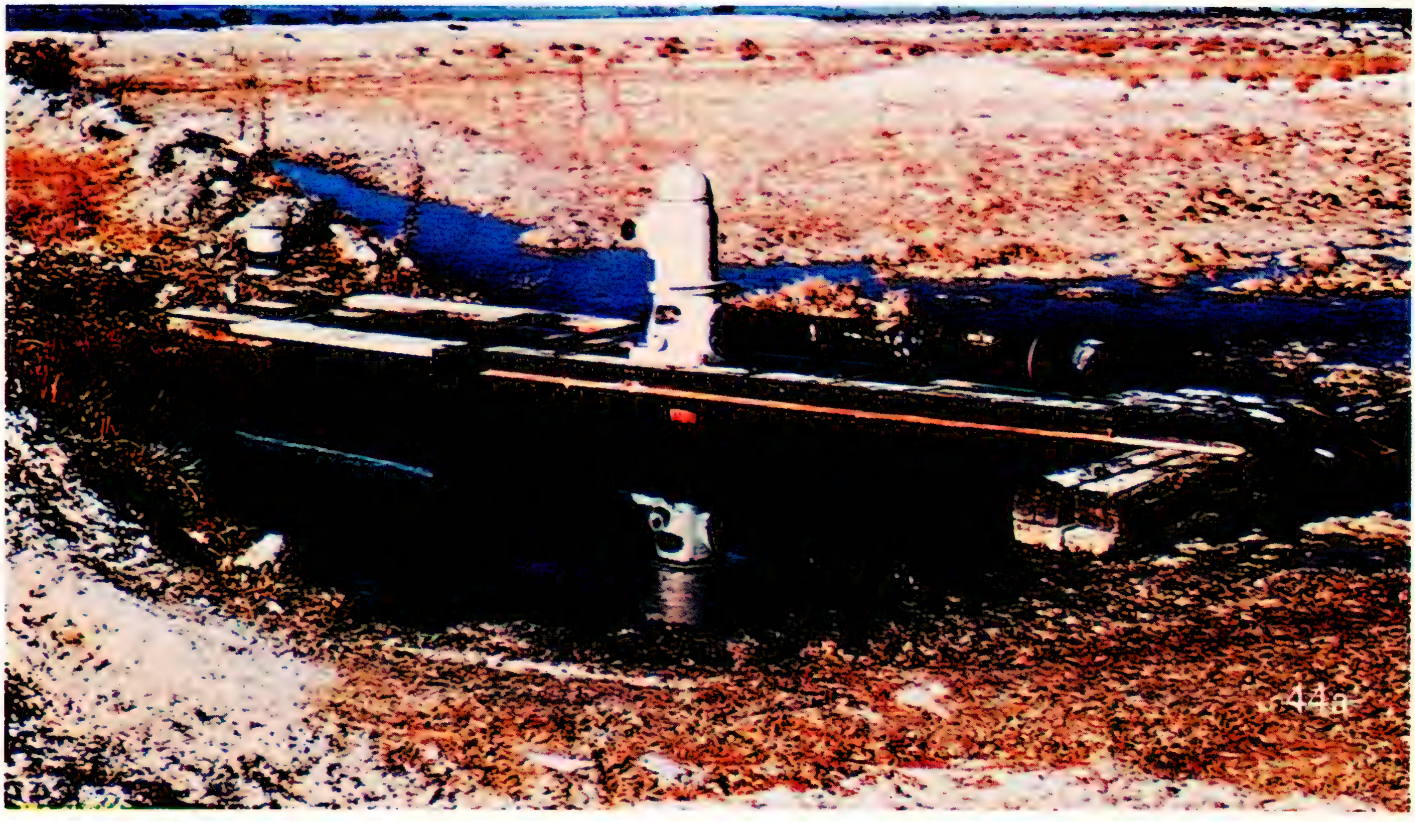

FIGURE 44a. Jackrabbit Spring, Ash Meadows, Nevada, with pump suspended directly over the spring. James Yoakum.
44b. Jackrabbit Spring after the pump was activated. James Yoakum.

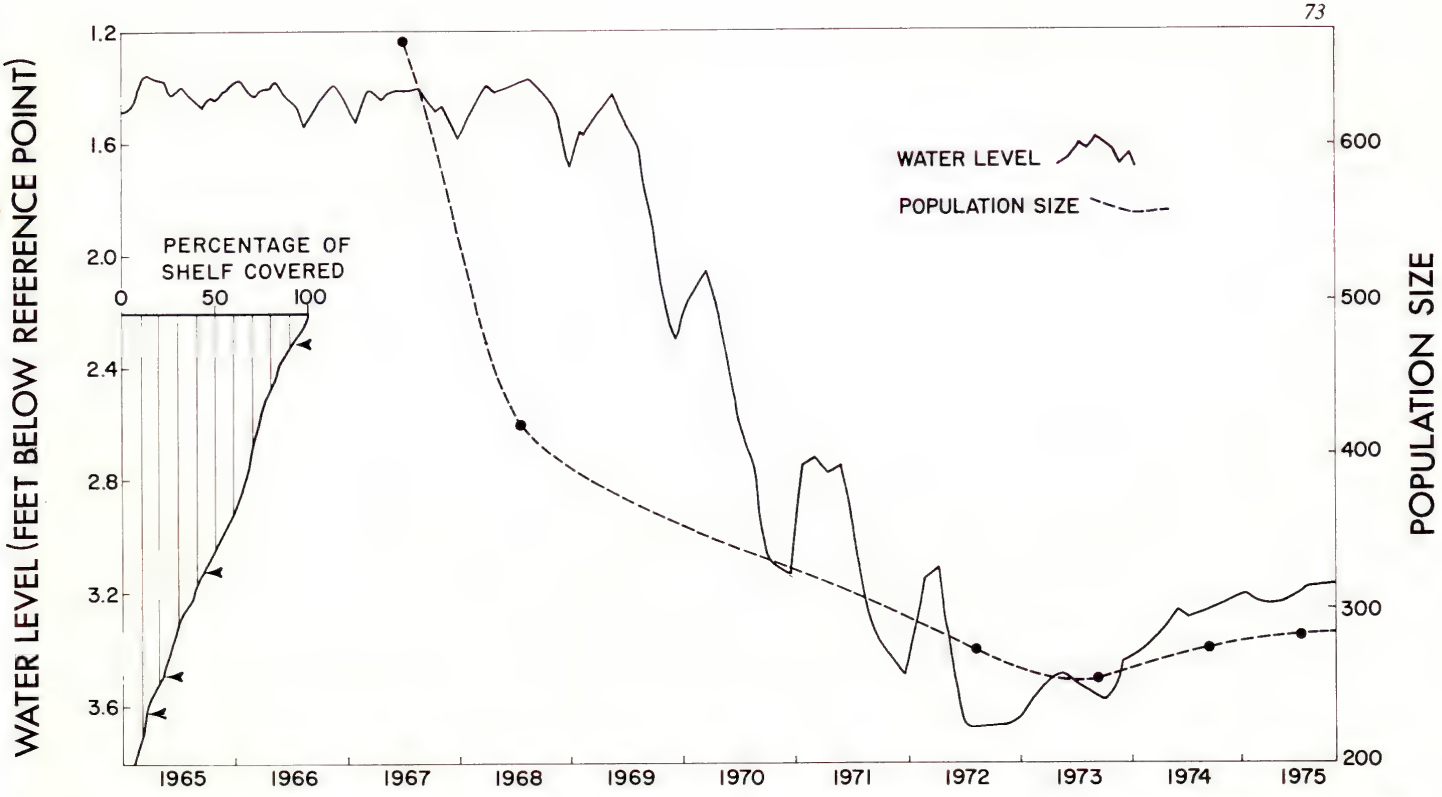

FIGURE 45. Decreasing water levels in Devils Hole as the result of nearby pumping for irrigation since 1968 has reduced the size of the Devils Hole pupfish population. Maximum midsummer population size drops dramatically as the water level and, consequently, the size of the spawning and feeding shelf is reduced. Since 1975 the water level has been maintained at a reduced but stable level, and the population has increased to nearly 400 individuals. (After Dudley and Larson, 1976).

FIGURE 46. Divers checking the fish population in Devils Hole. Alan Heller.

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FIGURE 47. Owens Valley Native Fish Sanctuary near Bishop, California. E.P. Pister.

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